

**EFFECTS OF EXPLOITATION, LOSS OF NURSERY HABITAT,
AND STOCKING ON THE DYNAMICS AND PRODUCTIVITY
OF LAKE TROUT POPULATIONS IN ONTARIO LAKES**

**Lake Trout Synthesis
Response to Stress Working Group
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ABSTRACT

Evans, D. O., J. M. Casselman, and C. C. Willox. 1990. Effects of exploitation, loss of nursery habitat, and stocking on the dynamics and productivity of lake trout in Ontario Lakes. Lake Trout Synthesis, Ont. Min. Nat. Resour., Toronto, Ont. 193 p.

We employed creel survey information, lake survey information, fisheries assessment data, and population modelling to evaluate the effects of angling exploitation, loss of deep-water nursery habitat, and stocking of hatchery-reared, non-native stocks of lake trout (*Salvelinus namaycush*) on the dynamics of lake trout populations in Ontario lakes. Variation in lake trout harvests between lakes is primarily caused by differences in fishing effort and lake size, but season, lake productivity, and habitat quantity and quality also have significant effects. Yields of lake trout in many Ontario lakes appear to be well in excess of the natural production capacity to sustain them, especially for winter fisheries on small lakes. In these cases, yields are often maintained by stocking of hatchery-reared fish, although harvest-per-unit-effort (HUE) is generally lower for populations supplemented by stocking than for self-sustaining wild populations. Fishing intensity and yield are highest on small lakes, but they also receive the highest stocking rates. Stocked lakes generally had less and lower quality habitat for lake trout than lakes supporting strong self-sustaining stocks, suggesting greater sensitivity of the former to overexploitation and other stressors. Angling pressure on lake trout was greatest during winter, winter fishing intensity being about 25% greater than spring and summer combined. Winter yield was similar to the yield for the entire open-water season, varying from about 1.16 kg ha⁻¹ for 100 ha lakes to about 0.10 kg ha⁻¹ for 10,000 ha lakes. Reductions in winter harvests appear to be required on lakes of about 1000 ha and less, if self-sustaining stocks are to be maintained. The relationship between yield and fishing intensity was similar during all seasons and provided a useful format for comparison of exploitation levels between lakes and for obtaining an assessment of the relative status of lake trout fisheries. Lake area was a good predictor of fishing effort, but a relatively weak predictor of harvests, the latter varying by 1-2 orders of magnitude for lakes of the same surface area. Harvest-per-unit-effort (HUE) in number of fish was inversely related to lake area for winter fisheries, despite higher fishing intensity in small lakes. HUE (kg) was positively related to lake area for open-water and annual fisheries. These results suggest either higher production or higher vulnerability of lake trout in small lakes during winter and reflect larger body sizes of lake trout in large lakes which are more heavily fished during open-water seasons. Use

of two rods per angler during winter appears to cause a significant increase in harvest per angler. This effect is greatest on small lakes.

Summer nursery habitat quantity and quality is a critical factor for natural production of self-sustaining stocks of lake trout. Young-of-the-year juvenile lake trout are found in deep water during summer, below the hypolimnetic depths inhabited by adult trout. Depth, temperature, and dissolved oxygen distributions for juvenile and adult lake trout were summarized from the published literature, and a habitat classification scheme proposed based on these variables. The essential habitat volume between 15.5°C and 4 mg L⁻¹ dissolved oxygen was termed the vital habitat for adult lake trout and 15.5°C to 2 mg L⁻¹ the habitable volume for all life stages. Seventy five habitat variables were developed and correlated with the stock status for lake trout in 212 inland Ontario lakes. Self-sustaining, native stocks were strongly associated with large vital and habitable volumes, and with high concentration of dissolved oxygen in the habitats occupied by adults and juveniles. The critical dissolved oxygen concentration of the deep-water nursery habitat, at which lake trout stocks become locally extinct, was about 2.3 mg L⁻¹. The corresponding concentration for summer adult habitat is about 3.1 mg L⁻¹, which is near the laboratory determined incipient lethal level for salmonids in general. Strong self-sustaining stocks of lake trout were found where mean oxygen concentrations of the adult and juvenile depth ranges were about 5.8 and 6.0 mg L⁻¹, respectively, at about 50% saturation. Comparable values for remnant self-supporting native stocks were 3.7 mg L⁻¹ and 4.0 mg L⁻¹, respectively. Nutrient additions from cottages, camp grounds, and municipalities that increase primarily productivity and lake metabolism, and cause hypolimnetic dissolved oxygen concentrations to fall below the incipient response threshold (about 6 mg L⁻¹) would be expected to lower the rate of production of self-sustaining lake trout populations by causing decreased scope for activity. Because of the cannibalistic behaviour of adult lake trout, recruitment is strongly density-dependent, providing some compensation for changes in both adult and early survival, but this mechanism serves primarily to regulate recruitment at high adult densities not to rectify changes in carrying capacity of the habitat for any particular life stage. Reduction in quantity and quality of the summer nursery habitat would be expected to result in increased interaction between juveniles and adults, and increased incidence of cannibalism and reduced recruitment.

Population modelling revealed marked sensitivity of lake trout populations to the combined effects of exploitation and reductions in early survival, exploitation being much more damaging to

populations having weak early survival. Protection of early life habitats, therefore, is extremely critical for maintenance of angling yields of self-sustaining lake trout populations. The population model also revealed the lengthy response times, in the order of decades, of lake trout populations to chronic degradation and conversely to rehabilitative measures, both of which clearly emphasize the benefits of effective fisheries assessment and conservation management of natural self-sustaining stocks.

Stocking tends to stimulate fishing which, in turn, can result in displacement of the local native stock by the hatchery stock. Modelling revealed that stocking of non-native lake trout, on wild populations subject to high exploitation rates, caused transformation of the genetic composition of the extant population, even when the stocked fish did not reproduce or interbreed with the native fish. Our model predicted that, at high exploitation and stocking rates presently seen in many Ontario lakes, the wild stocks would be replaced by the hatchery stock within a few generations. Widespread stocking of a few domesticated non-native stocks, therefore, appears to pose a serious risk to the genetic diversity of the species. We recommend a moratorium on widespread supplemental stocking of self-sustaining wild stocks. We also recommend that greater emphasis be placed on management for self-sustaining status of the lake trout resource. The best way to achieve this objective is through regulation of exploitation to allow adequate spawning escapement combined with habitat conservation and rehabilitation.



INTRODUCTION

Among the stressors that operate on lake trout (*Salvelinus namaycush*) populations, three are of particular concern to fisheries managers: excessive exploitation; habitat degradation; and species introductions, including stocking of hatchery fish (Evans et al. 1991). The first two, exploitation and habitat loss, are widely suspected among fisheries biologists to be the major causes of declining lake trout stocks in Ontario (Lewis et al. 1990). Our objectives were to investigate the effects of these factors on lake trout in Ontario lakes. Stocking is not generally recognized as a stressor, in part, because it is widely employed as a management technique to counteract population declines caused by fishing and various types of habitat loss. More importantly though, the potential stress effects of stocking are counter intuitive in that stocking generally does not result in fewer fish, at least not in the short-term. An important concern is that stocking does not always result in an increase in the number of fish either. The effects of stocking, however, have more to do with biological and genetic processes that are not readily observable than with the number of fish produced. We have included consideration of stocking as a stressor, because of the potential that commonly employed stocking practices have for causing subtle, but serious degradation of the native lake trout resource.

Exploitation, loss of early life habitat, and stocking of hatchery reared lake trout are examined in some detail in the following sections. Specific questions and hypotheses are addressed concerning the ways in which these factors operate on lake trout populations and the effects that they have on population dynamics and production. We have employed two approaches: (1) analysis of empirical field data from long-term population studies on Lake Opeongo obtained from records of the Ontario Ministry of Natural Resources (OMNR), and from the Aquatic Habitat Inventory Data Base (AHIDB) and the Lake Trout Synthesis Summary Data Base (LTSSDB) compiled from OMNR District, Fisheries Assessment Unit (FAU), and Fisheries Research Section surveys of lake trout angling fisheries and lakes; and (2) development of a simulation model for a hypothetical lake trout population. The simulation model, which is based on data from the Lake Opeongo lake trout population, has been used to explore population responses to varying rates of fishing, variation in early survival, and stocking of hatchery-reared lake trout. The model has also been used to explore three hypothetical development scenarios and five hypothetical rehabilitation scenarios.

ANGLING EXPLOITATION OF LAKE TROUT

We have compiled and analysed lake trout creel survey data for Ontario lakes to assess the range of harvest, yield and fishing intensity. **Harvest is defined as the number or weight of fish removed per unit time, yield is the number or weight of fish removed per unit area per unit time, and fishing intensity is the fishing effort per unit area per unit time.** Our objective was to provide a basis for comparison of these exploitation statistics between lakes and to investigate the effects of various factors on lake trout yields. Fishing effort and lake size are the primary factors influencing harvest and yield of lake trout angling fisheries (McCombie 1983; Goddard et al. 1987). For each of the major fishing seasons (winter, spring, and summer), we have described predictive equations relating harvest and yield in terms of effort and area for all Ontario lake trout lakes for which suitable seasonal data exists. These equations and graphic representations provide a basis for local fisheries managers to compare the fisheries of familiar and new lakes against a provincial lake set. We have used these data to assess the influences of lake size; habitat variables (mean depth and nursery habitat), lake productivity (total dissolved solids (TDS) and water clarity), and stocking on the yields of Ontario lake trout populations. Improved understanding of the influence of these variables on fishing and harvest is needed to evaluate the dynamics of recreational angling as a stressor of lake trout populations.

SOURCES OF DATA AND METHODOLOGY

Information concerning lake trout angling fisheries was taken from the LTSSDB. In order to ensure a standardized data set that would enable valid statistical comparisons between lakes, certain criteria were established for inclusion of creel survey data in our analyses. First, we limited our analyses to fishing effort and harvest data that were based on fisheries for lake trout only. Second, only creel surveys which reported the actual time and duration of the creel survey period were used. Where the survey duration was indicated, the reported estimates for effort and harvest was assumed to be for the survey period. Estimated effort and harvest in number and weight of fish for each creel survey were then corrected to a standard fishing day by dividing the total estimate (effort or harvest) by the number of days of the survey. A creel survey record was not used in the analyses, if any of the information or estimates provided in the data base for that survey were classified as uncertain. The type of fishing effort, either angler-hours or rod-hours, had to be specified for inclusion of a

winter creel survey in any of the analyses. Angler-hours and rod-hours were assumed to be equivalent for surveys during other seasons of the year, because only one rod can legally be used during open-water seasons.

Selection and standardization of the data in this way reduced the number of creel surveys in the data base from a total of 1480 to 502 for which statistics for lake trout-specific fisheries were available. Of these, 227 surveys were of known duration and dates where angler effort was given in angler-hours, while 221 surveys were available with effort in rod-hours.

Multiple years of creel data for a given lake were combined into a single mean value by taking the means of the $\log_{10}$ transformed estimates for individual years. In all subsequent regression analyses, analysis of variance (ANOVA) and analysis of covariance (ANCOVA) estimates for individual lakes were weighted using the number of years of survey data. Variance could not be used as a weighting factor because many surveys involved only one year of data.

The creel survey data were further divided into seasons of the year, winter, spring and summer corresponding to January to March, May to June, and July to September inclusive, respectively. Surveys that extended into an adjacent season by up to one month were included with the main season to which they applied rather than attempting to partition the estimates. Thus, some overlap between seasons occurs in the data. Winter is assumed to be synonymous with ice fishing and spring, summer and fall are assumed to represent open-water fisheries. For purposes of our analyses, open-water fisheries are those designated as such in the LTSSDB. We have also combined data for spring and summer fisheries on a given lake into single estimates for the open-water season, when data were available for both seasons within the same years.

Estimates of annual harvest were taken directly as reported from the LTSSDB. We have not attempted to combine estimates from single seasons to obtain total annual estimates or to provide annual estimates for lakes with single season fisheries. Annual estimates in the data base are not accompanied by information on season duration or the number of seasons actually fished. In some cases annual catches represent open-water fisheries only because of winter closures on some lakes, notably those in Algonquin Provincial Park.

Analyses are based on surveys of populations having varied histories. Each population has been classified according to its reproductive status (i.e. self-sustaining versus artificial recruitment), stocking history, and whether it is extant or extinct (Table 1). The population categories are the same as those in Evans et al. (1991), except for I3, and are taken from Lewis et al. (1990).

Appendix A provides a complete listing of all lakes used in analyses of creel survey information, including their watershed designation, latitude, longitude and elevation. Additional physical and chemical data for the lakes are given in Appendix B and information about development, introductions, and stocking is given in Appendix C. Information in Appendix C is summarized from the Lake Trout Questionnaire (Lewis et al. 1990) and the OMNR Fish Stocking Data Base (Fish Culture Section, Fisheries Branch, OMNR, Toronto).

TABLE 1. Categories describing the status of lake trout populations based on origin, stocking, reproduction, and recruitment. With the exception of I3, categories are similar to those used in Evans et al. (1991).

Atlas	Numerical code	Description
N1	1	Native population: natural reproduction, self-sustaining, unstocked
N3	3	Native population: some natural reproduction; partly self-sustaining; supplemented by stocking of non-native stock
N5	5	Native population; little or no reproduction; population maintained by stocking of non-native stock
N6	6	Native remnant population; some natural reproduction; may be self-sustaining; supplemented by stocking of F_1 splake
I1	7	Introduced population; natural reproduction; self-sustaining
I2	8	Introduced population; some natural reproduction; partly self-sustaining; supplemented by stocking
I3	9	Introduced population; little or no natural reproduction; not self-sustaining; stocking not continued
E	10	Extinct population; native or introduced population which disappeared after known period of natural recruitment
L	11	Lost population; population of unknown history and reproductive status which disappeared

FACTORS AFFECTING ANGLING, HARVESTS, AND YIELDS

Fishing Effort and Harvest

Figures 1-6 illustrate the relationships between fishing effort and harvest in numbers and kilograms of fish for each of the major fishing seasons. Extreme deviations below the fitted regression lines suggest lower than expected harvests and the possibility of either low productivity or a stress factor operating on the population. These curves provide a first order diagnostic of the productivity of a lake trout population and the possible presence of a stressor. Conversely, large positive deviations indicate either excessive short-term harvests, or exceptionally productive lake trout lakes if the harvest levels are being sustained. The residuals for the harvest versus effort regressions for winter (angler-hours and rod-hours), spring, summer, and open-water seasons are also given (Appendix D). The residuals from the least-squares harvest-effort regressions provide an indication of the relative production status of lake trout for individual lakes. This presentation allows one to easily compare seasonal and annual harvests of lake trout between lakes, thereby identifying deviant or anomalous cases. This approach provides a provincial data set for comparisons of empirical lake trout harvests and efforts. Similar data from other lakes can be easily compared with and added to the existing data set. Relative performance of lake trout, obtained by comparison with the harvest-effort equations, provides a useful indication of the relative yield status of a stock. A standard statistical procedure can be used to test suspiciously large individual, non-randomly drawn deviation to see if it falls within the expected sampling error ($t = \hat{Y} \cdot Y / S_{Y \cdot \hat{Y}}$). In this procedure, Y is the actual harvest estimate of the suspicious case to be tested, $\hat{Y}$ is the expected harvest for the suspicious case, based on the regression with the suspicious observation omitted, and $S_{Y \cdot \hat{Y}}$ is the standard deviation due to sampling errors for the new regression. Other criteria could also be established for identification of suspicious observations, but in all cases, supplement information would be needed for effective evaluation of the status of the fishery.

Fishing effort has been found to be the single most important determinant of harvest in lake trout angling fisheries in Ontario lakes, effort accounting for 73% of the annual variation in angler catch between lakes (Goddard et al. 1987). Harvest-effort relationships for various fishing seasons are given in Tables 2-6. Total fishing effort explained 70% and 79% of the variation in annual harvest in number and weight (kg) of lake trout, respectively (Fig. 6, Table 6). Similar amounts of variation

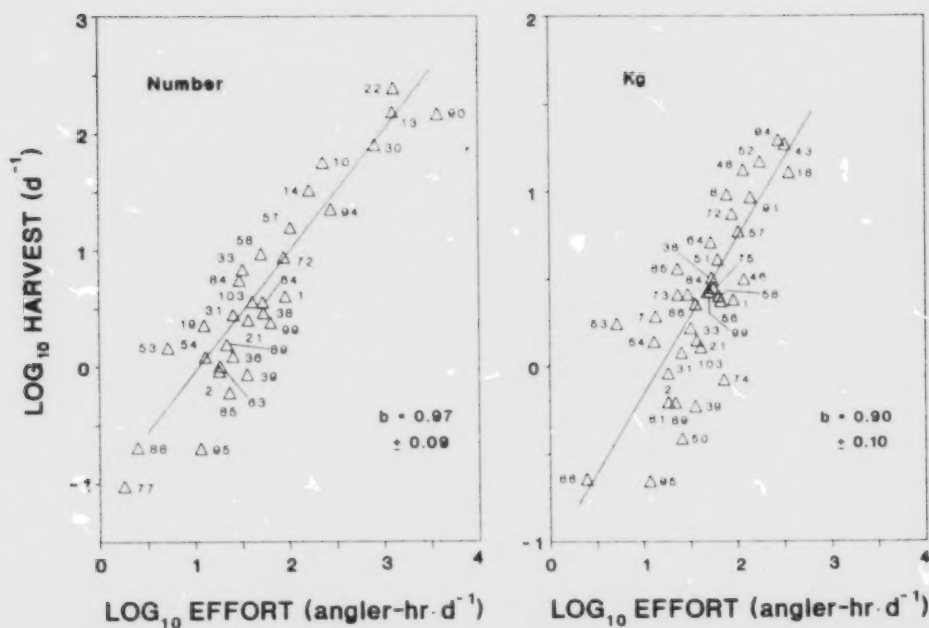


FIG. 1. The relationship between harvest in number and kilograms of lake trout per day and fishing effort in angler-hours per day during winter. The numbers opposite the symbols refer to lakes described in Appendices A, B, and C.

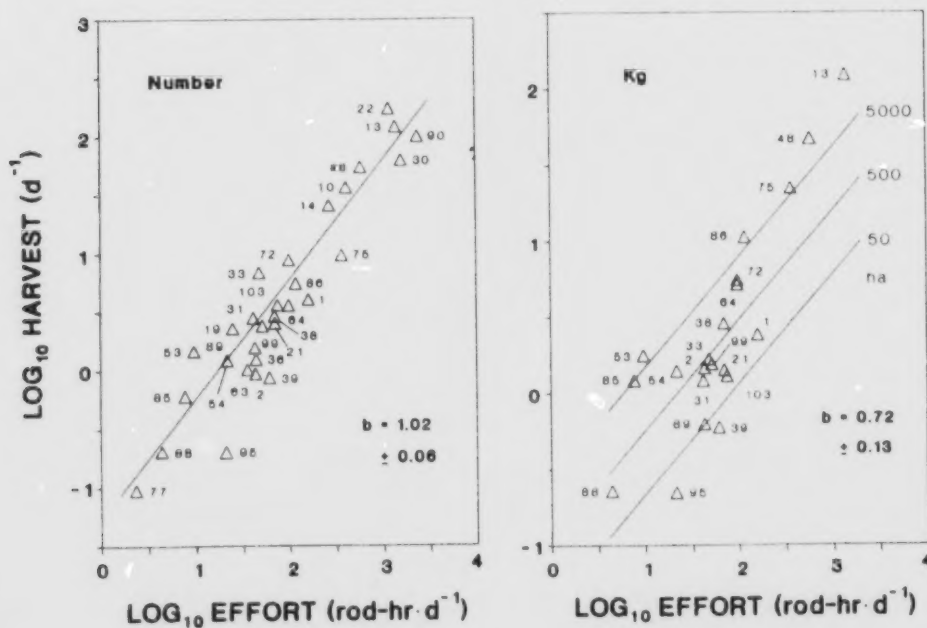


FIG. 2. The relationship between harvest in number and kilograms of lake trout per day and fishing effort in rod-hours per day during winter. The numbers opposite the symbols refer to lakes described in Appendices A, B, and C.

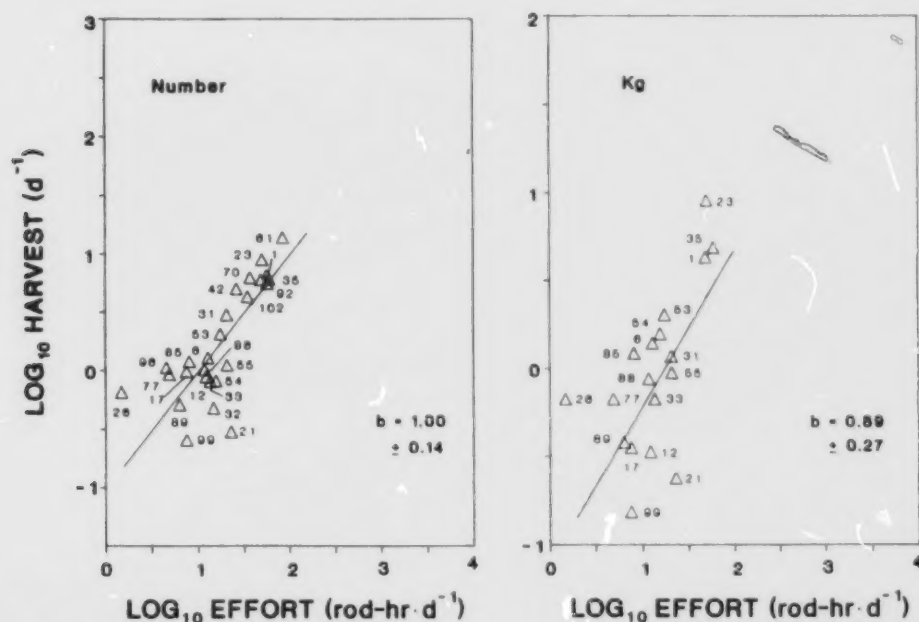


FIG. 3. The relationship between harvest in number and kilograms of lake trout per day and fishing effort in rod-hours per day during spring. The numbers opposite the symbols refer to lakes described in Appendices A, B, and C.

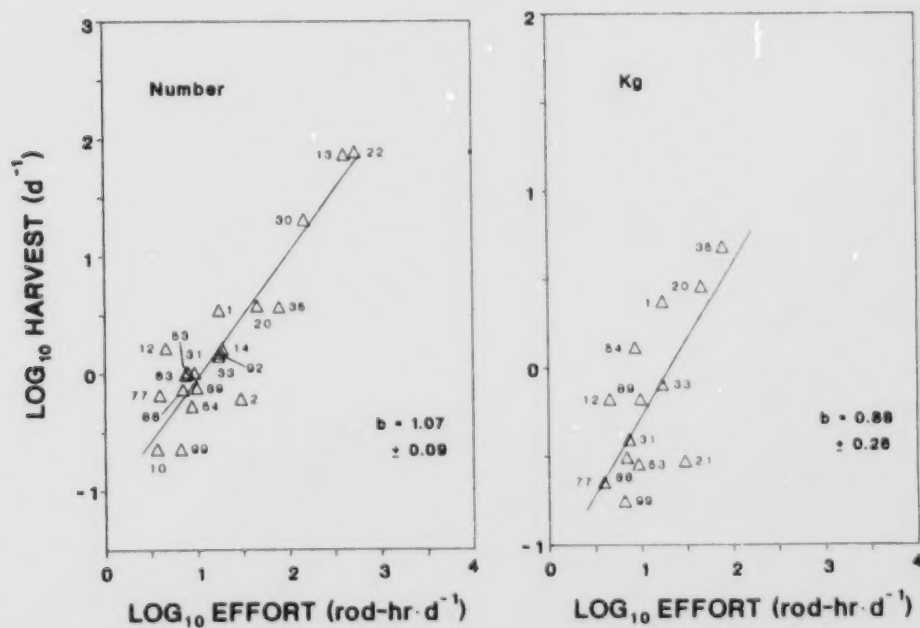


FIG. 4. The relationship between harvest in number and kilograms of lake trout per day and fishing effort in rod-hours per day during summer. The numbers opposite the symbols refer to lakes described in Appendices A, B, and C.

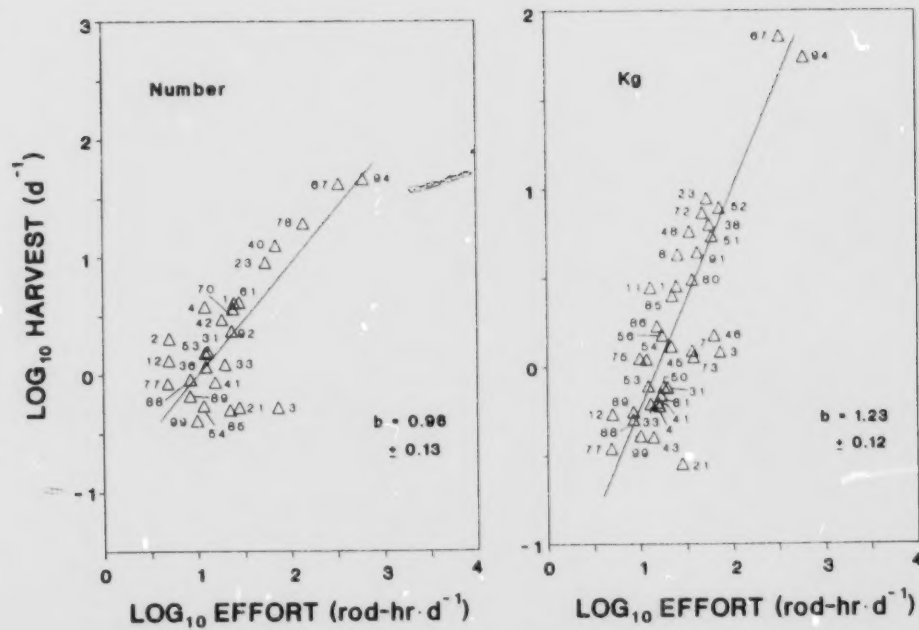


FIG. 5. The relationship between harvest in number and kilograms of lake trout per day and fishing effort in rod-hours per day during open water. The numbers opposite the symbols refer to lakes described in Appendices A, B, and C.

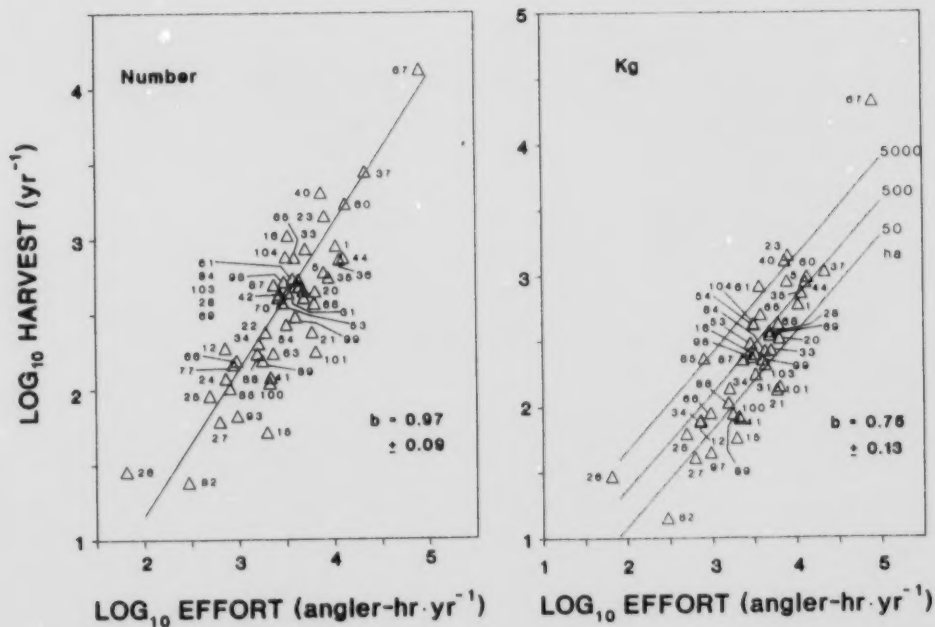


FIG. 6. The relationship between harvest in number and kilograms of lake trout per year and fishing effort in angler-hours per year. The numbers opposite the symbols refer to lakes described in Appendices A, B, and C.

TABLE 2. Summary of empirical regression statistics (intercept (a), slope (b), standard error of b, probability of a type 1 error (P), variation explained by the independent variate (r^2)) for relationships between lake trout harvest, fishing effort, lake area and morphoedaphic index for winter angling fisheries in Ontario lakes. Data are for the period January, February, and March. All effort and harvest statistics are given in daily rates.

Variables		# of lakes	Regression statistics				
Dependent	Independent		a	b	Sb	P	r ² %
Winter							
Simple regressions							
log harvest (n)	log effort (rod hr)	30	-1.25	1.02	0.06	<0.01	91
log harvest (kg)	log effort (rod hr)	21	-1.33	0.96	0.13	<0.01	73
log harvest (n)	log effort (angler hr)	31	-1.01	0.97	0.09	<0.01	81
log harvest (kg)	log effort (angler hr)	37	-1.06	0.90	0.10	<0.01	68
log harvest (n)	log area (ha)	31	-1.43	0.68	0.16	<0.01	35
log harvest (kg)	log area (ha)	37	-0.56	0.35	0.13	<0.05	15
log yield (n)	log effort ha ⁻¹ (rod hr)	30	-1.29	1.03	0.09	<0.01	83
log yield (n)	log effort ha ⁻¹ (angler hr)	31	-1.14	0.94	0.08	<0.01	73
log yield (n)	log area (ha)	31	-1.43	0.32	0.16	0.61	9
log yield (n)	log MEI	31	-2.47	0.27	0.37	0.47	0
log yield (kg)	log effort ha ⁻¹ (rod hr)	21	-1.78	0.65	0.11	<0.01	61
log yield (kg)	log effort ha ⁻¹ (angler hr)	37	-1.41	0.86	0.07	<0.01	79
log yield (kg)	log area (ha)	37	-0.56	-0.65	0.13	<0.01	40
log yield (kg)	log MEI	32	-2.56	0.28	0.33	0.40	0
log effort (rod hr)	log area	30	-0.01	0.70	0.17	<0.01	35
log effort ha ⁻¹ (rod hr)	log area	30	-0.02	0.30	0.17	0.08	7
log effort (angler hr)	log area	47	0.30	0.47	0.12	<0.01	24
log effort ha ⁻¹ (angler hr)	log area	47	0.31	-0.53	0.12	<0.01	27
Multiple regressions							
log harvest (n)	log effort (angler hr)	31	-1.01	0.97	0.09	<0.01	81
	log area (ha)					ns	
log harvest (kg)	log effort (angler hr)	37	-1.06	0.90	0.10	<0.01	68
	log area (ha)					ns	
log harvest (n)	log effort (rod hr)	30	-1.26	1.02	0.06	<0.01	91
	log area					ns	
log harvest (kg)	log effort (rod hr)	21	-2.09	0.72	0.13	<0.01	74
	log area			0.42	0.13	<0.01	9
log yield (n)	log effort ha ⁻¹ (angler hr)	31	-1.14	0.94	0.08	<0.01	73
	log area (ha)					ns	
log yield (kg)	log effort ha ⁻¹ (angler hr)	37	-1.41	0.86	0.07	<0.01	79
	log area (ha)					ns	

TABLE 3. Summary of empirical regression statistics (intercept (a), slope (b), standard error of b, probability of a type 1 error (*P*), variation explained by the independent variate (*r*²)) for relationships between lake trout harvest, fishing effort, lake area and morphoedaphic index for spring angling fisheries in Ontario lakes. Data are for the spring period, April, May, and June. All effort and harvest statistics are given in daily rates.

Variables		# of lakes	Regression statistics				
Dependent	Independent		a	b	Sb	P	r ² %
Spring							
Simple regressions							
log harvest (n)	log effort	25	-1.02	1.00	0.14	<0.01	67
log harvest (kg)	log effort	18	-1.12	0.89	0.27	<0.01	36
log harvest (n)	log area	25	-1.03	0.47	0.20	<0.05	16
log harvest (kg)	log area	18	-0.74	0.24	0.23	0.32	0
log yield (n)	log effort ha ⁻¹	25	-0.65	1.25	0.15	<0.01	74
log yield (n)	log area	25	-1.02	-0.54	0.20	<0.05	21
log yield (n)	log MEI	25	-2.20	-0.49	0.43	0.27	1
log yield (kg)	log effort ha ⁻¹	18	-0.97	1.18	0.23	<0.01	60
log yield (kg)	log area	18	-0.73	-0.76	0.23	<0.01	37
log yield (kg)	log MEI	18	-2.58	-0.16	0.55	0.75	0
log effort	log area	25	-0.34	0.59	0.13	<0.01	44
log effort ha ⁻¹	log area	25	-0.33	-0.41	0.13	<0.01	27
Multiple regressions							
log harvest (n)	log effort	25	-1.02	1.00	0.14	<0.01	67
	log area					ns	
log harvest (kg)	log effort	18	-1.12	0.89	0.27	<0.01	36
	log area					ns	
log yield (n)	log effort ha ⁻¹	25	-0.65	1.25	0.15	<0.01	74
	log area					ns	
log yield (kg)	log effort ha ⁻¹	18	-0.97	1.18	0.23	<0.01	60
	log area					ns	

TABLE 4. Summary of empirical regression statistics (intercept (a), slope (b), standard error of b, probability of a type 1 error (*P*), variation explained by the independent variate (*r*²)) for relationships between lake trout harvest, fishing effort, lake area and morphoedaphic index for summer angling fisheries in Ontario lakes. Data are for the summer period, July, August, and September. All effort and harvest statistics are given in daily rates.

Variables		# of lakes	Regression statistics				
Dependent	Independent		a	b	Sb	P	r ² %
Summer							
Simple regressions							
log harvest (n)	log effort	20	-1.11	1.07	0.09	<0.01	89
log harvest (kg)	log effort	13	-1.16	0.88	0.26	<0.01	46
log harvest (n)	log area	20	-2.98	1.20	0.23	<0.01	58
log harvest (kg)	log area	13	-1.89	0.64	0.31	0.06	21
log yield (n)	log effort ha ⁻¹	20	-0.71	1.22	0.15	<0.01	75
log yield (n)	log area	20	-2.95	0.19	0.23	0.42	0
log yield (n)	log MEI	20	-2.77	0.66	0.32	0.06	14
log yield (kg)	log effort ha ⁻¹	13	-1.19	1.06	0.39	<0.05	34
log yield (kg)	log area	13	-1.67	-0.45	0.32	0.18	7
log yield (kg)	log MEI	13	-2.87	0.09	0.43	0.83	0
log effort	log area	20	-1.93	1.19	0.16	<0.01	73
log effort ha ⁻¹	log area	20	-1.90	0.18	0.16	0.28	1
Multiple regressions							
log harvest (n)	log effort	20	-1.11	1.07	0.09	<0.01	89
	log area					ns	
log harvest (kg)	log effort	13	-1.16	0.88	0.26	<0.01	46
	log area					ns	
log yield (n)	log effort ha ⁻¹	20	-0.71	1.22	0.15	<0.01	75
	log area					ns	
log yield (kg)	log effort ha ⁻¹	13	-1.19	1.06	0.39	<0.05	34
	log area					ns	

TABLE 5. Summary of empirical regression statistics (intercept (a), slope (b), standard error of b, probability of a type 1 error (P), variation explained by the independent variate (r^2)) for relationships between lake trout harvest, fishing effort, lake area and morphoedaphic index for open-water angling fisheries in Ontario lakes. Data are for the open-water period, April to September. All effort and harvest statistics are given in daily rates.

Variables		# of lakes	Regression statistics				
Dependent	Independent		a	b	Sb	P	r ² %
Open water							
Simple regressions							
log harvest (n)	log effort	26	-0.97	0.96	0.13	<0.01	67
log harvest (kg)	log effort	37	-1.47	1.23	0.12	<0.01	73
log harvest (n)	log area	26	-1.80	0.74	0.14	<0.01	51
log harvest (kg)	log area	37	-1.28	0.51	0.14	<0.01	24
log yield (n)	log effort ha ⁻¹	26	-1.15	0.92	0.23	<0.01	38
log yield (n)	log area	26	-1.79	-0.26	0.14	0.06	8
log yield (n)	log MEI	26	-2.33	-0.55	0.30	0.08	8
log yield (kg)	log effort ha ⁻¹	37	-1.27	0.92	0.10	<0.01	71
log yield (kg)	log area	37	-1.28	-0.49	0.14	<0.01	23
log yield (kg)	log MEI	30	-2.89	0.41	0.35	0.26	1
log effort	log area	47	0.33	0.35	0.09	<0.01	22
log effort ha ⁻¹	log area	47	0.34	-0.65	0.09	<0.01	50
Multiple regressions							
log harvest (n)	log effort	26	-0.97	0.96	0.13	<0.01	67
	log area					ns	
log harvest (kg)	log effort	37	-1.47	1.23	0.12	<0.01	73
	log area					ns	
log yield (n)	log effort	26	-1.15	0.92	0.23	<0.01	38
	log area					ns	
log yield (kg)	log effort	37	-1.76	1.14	0.14	<0.01	72
	log area			0.28	0.12	<0.05	4

TABLE 6. Summary of empirical regression statistics (intercept (a), slope (b), standard error of b, probability of type 1 error (P), variation explained by the independent variate (r^2)) for relationships between lake trout harvest, fishing effort, lake area and morphoedaphic index for annual angling fisheries in Ontario lakes. Data are for the whole year. All effort and harvest statistics are given in daily rates.

Variables		# of lakes	Regression statistics				
Dependent	Independent		a	b	Sb	P	r ² %
Annual							
Simple regressions							
log harvest (n)	log effort	49	-0.78	0.97	0.09	<0.01	70
log harvest (kg)	log effort	43	-1.28	1.07	0.08	<0.01	79
log harvest (n)	log area	49	1.26	0.53	0.10	<0.01	37
log harvest (kg)	log area	43	0.60	0.72	0.07	<0.01	69
log yield(n)	log effort ha ⁻¹	49	-0.92	1.05	0.10	<0.01	67
log yield (n)	log area	49	1.26	-0.47	0.10	<0.01	32
log yield (n)	log MEI	48	0.08	0.06	0.22	0.80	0
log yield (kg)	log effort ha ⁻¹	43	-0.78	0.71	0.09	<0.01	58
log yield (kg)	log area	43	0.60	-0.28	0.07	<0.01	24
log yield (kg)	log MEI	42	-0.08	-0.00	0.17	0.99	0
log effort	log area	49	2.05	0.56	0.07	<0.01	57
log effort ha ⁻¹	log area	49	2.05	-0.44	0.07	<0.01	45
Multiple regressions							
log harvest (n)	log effort	49	-0.78	0.97	0.09	<0.01	70
	log area					ns	
log harvest (kg)	log effort	43	-0.89	0.74	0.13	<0.01	80
	log area			0.29	0.09	<0.01	4
log yield (n)	log effort ha ⁻¹	49	-0.92	1.05	0.10	<0.01	67
	log area					ns	
log yield (kg)	log effort ha ⁻¹	43	-0.78	0.71	0.09	<0.01	58
	log area					ns	

in harvest were explained by effort within various seasons of the year (Tables 2-5), although spring and summer r^2 values for harvest in weight (36 and 46%, respectively) were notably lower. This was probably due to much smaller sample sizes for harvests in weight during those seasons (Tables 3 and 4).

Lake area, when included with fishing effort, had a significant effect on harvest in weight only for the winter (Fig. 2) and annual (Fig. 7) periods, explaining 9% and 4%, respectively, of the total variations in harvest in those seasons (Tables 2 and 6). Annual effort increased in proportion to area to the power 0.56. Similarly, winter effort increased with area to the power 1.19, suggesting greater relative effort on large lakes during that season. This corresponds to increased summer fishing effort on large lakes associated with tourist and cottage activities that are more prevalent on the larger lakes. Seasonal comparisons of effort-area relationships revealed that fishing effort was much greater during winter than during either spring or summer on small lakes (100 ha). Effort during spring was greater than during summer on small lakes, but was much greater during summer on large lakes. Harvests generally followed the same patterns as effort being highest during winter, intermediate during spring, and lowest during summer in small lakes. In large lakes, harvests were highest during summer, intermediate during winter, and lowest during spring. Total efforts and yields for winter, spring, and summer are roughly similar to the annual estimates only for lakes of 1000 ha (Table 7). Variation in the slopes of the area relationships resulted in poor agreement between seasonal totals and annual estimates for small and large lakes (i.e. 100 and 10,000 ha) (Table 7).

Comparison of the estimated annual efforts and yields for lakes of 100 to 10,000 ha, based on five lakes having sustained yields over several years, was compared with annual efforts and harvests of all lakes in our data set. The five lakes (Bone, Chiblow-Denman, Christman, Flack, and Opeongo), spanning a size range from 58 to 5860 ha, support self-sustaining native populations of lake trout and have been identified by Payne et al. (1990) and Lester et al. (1991) as lakes representative of maximum sustained harvests for lake trout by virtue of sustaining stable harvests and population attributes under a history (12-16 yr) of moderate to heavy fishing pressure. Efforts and yields for these lakes, therefore, represent a "reference" for Ontario lake trout lakes, characteristic of maximum self-sustained yields (MSY) for relatively pristine lake trout habitats.

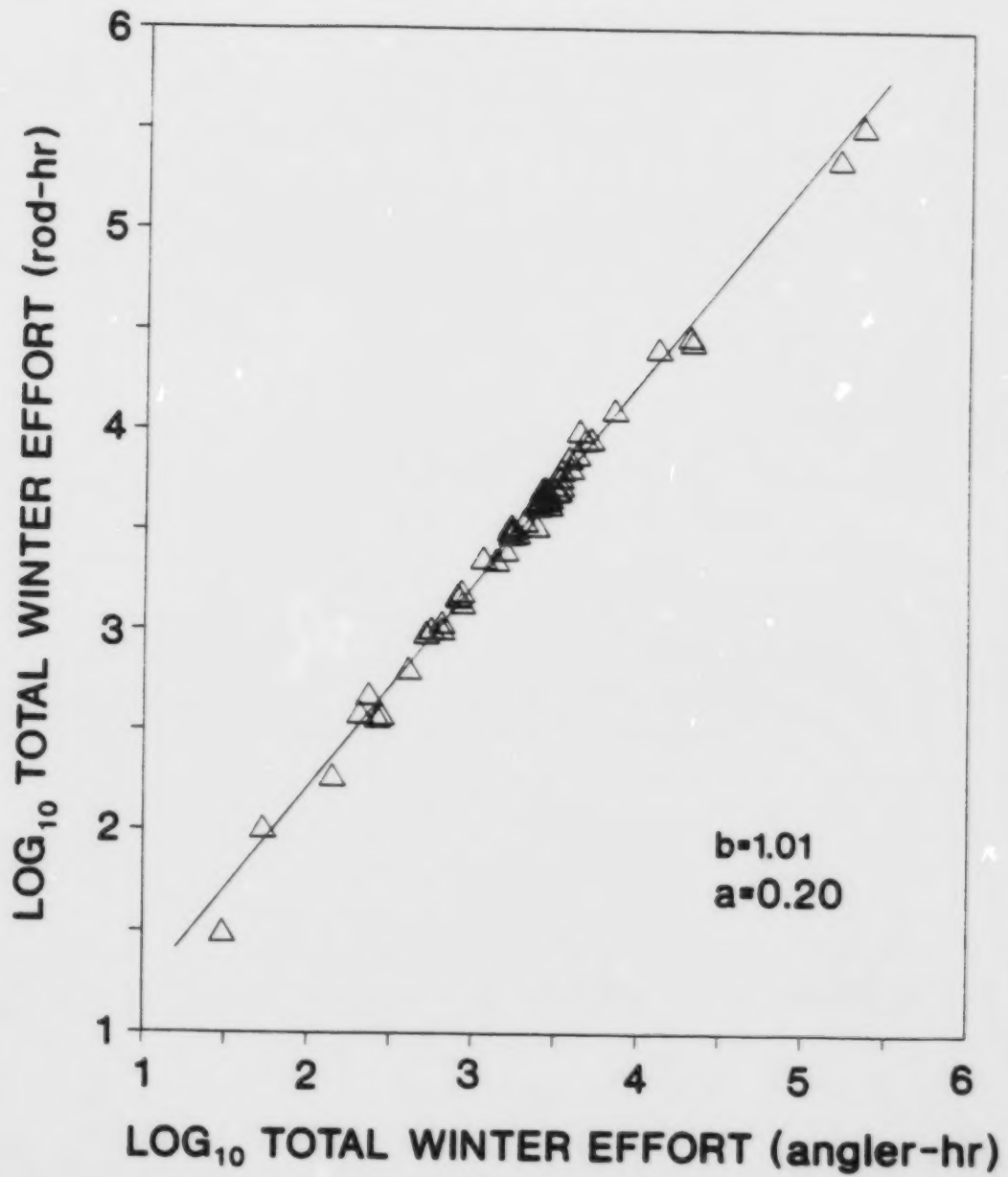


Fig. 7. The relationship between $\log_{10}$ total fishing effort during winter in rod-hours and $\log_{10}$ total fishing effort in angler-hours. The slope (b) and intercept (a) are shown.

TABLE 7. Summary of relationships between effort, harvest in numbers of fish, and weight of fish in kilograms and lake area for lake trout angling fisheries during various seasons of the year. Season duration for spring excludes April because of unfishable ice conditions.

Season	Dependent variable	Regression statistics				Lake area (ha)		
		n	a	b	r ²	100	1000	10,000
Winter (90)	Effort (hr)	47	0.30	0.47	0.24	1564	4616	13622
	Harvest (no)	31	-1.43	0.68	0.35	77	367	1755
	Harvest (kg)	37	-0.56	0.35	0.15	124	278	623
Spring (61)	Effort (hr)	25	-0.34	0.59	0.44	422	1642	6387
	Harvest (no)	25	-1.03	0.47	0.16	50	146	432
	Harvest (kg)	18	-0.74	0.24	0.00		45	
Summer (92)	Effort (hr)	20	-1.93	1.19	0.73	259	4016	62200
	Harvest (no)	20	-2.98	1.20	0.58	24	384	6078
	Harvest (kg)	13	-1.89	0.64	0.21	23	99	430
Open water (153)	Effort (hr)	26	0.33	0.35	0.22	1639	3670	8217
	Harvest (no)	26	-1.80	0.74	0.51	73	402	2212
	Harvest (kg)	37	-1.28	0.51	0.24	84	272	880
Annual (all lakes)	Effort (hr)	49	2.05	0.56	0.57	1479	5370	19498
	Harvest (no)	49	1.26	0.53	0.37	209	708	2399
	Harvest (kg)	43	0.60	0.72	0.69	104	575	3019
Annual (maximum sustainable harvest)	Effort (hr)	5	1.98	0.62	0.89	1621	6682	27542
	Harvest (no)	5	1.49	0.54	0.69	372	1288	4451
	Harvest (kg)	5	0.622	0.79	0.96	158	966	5920

Yields for all lakes (stocked and unstocked combined) in the annual data set were 40-60% lower at all lake sizes than MSY for the selected lakes, even though fishing effort was only 13-20% lower for all lakes combined. Analysis of covariance revealed that stocked and unstocked lakes did not have significantly different ($P = 0.5$) effort-area or harvest-area relationships for winter, open-water, or annual fisheries, therefore data for stocked and unstocked populations were combined for purposes of Table 7. Maximum sustained yields for the selected lake set cannot be used as a standard for all lakes, but rather as a general reference for highly productive self-sustaining populations. The five populations are not homogenous in terms of growth rates, maturation schedules, or longevity (Payne et al. 1990), but their lakes do provide high quality habitat and are highly productive for lake trout, producing from 0.59 kg ha⁻¹yr⁻¹ (Chiblow Lake) to 3.0 kg ha⁻¹yr⁻¹ (Bone Lake), compared to the

geometric mean for all lakes of $0.76 \text{ kg ha}^{-1}\text{yr}^{-1}$ ($\pm 95\%$ confidence interval: $0.49\text{--}1.9 \text{ kg ha}^{-1}\text{yr}^{-1}$), which includes harvests for many stocked lakes.

The slopes of the harvest-effort relationships, when expressed in angler-hours, were very near unity, indicating a linear relationship between harvest and effort (Tables 2-6) with exceptions of harvests in weight during the winter and annual surveys, where the slopes were less than unity (Tables 2 and 6), indicating a declining HUE as effort increases. Winter regressions of harvest versus effort in rod-hours have smaller intercepts than winter regressions expressed in angler-hours, which simply reflects the use of more than one fishing line per angler. Given that winter anglers may legally use two fishing lines and that existing winter creel survey data are often reported using both measures of effort (i.e. rod-hours and angler-hours), we have summarized the data using both of these statistics. The relationship between winter angling effort in angler-hours and rod-hours is shown in Fig. 7. The slope of the regression is not significantly different from one, but the intercept of 0.20 indicates that each angler-hour is equivalent to 1.58 rod-hours (i.e. $\text{antilog } 0.20$). Thus, over the range of observed effort for lakes in this data set, winter anglers on average use 1.58 lines. Further discussion of rod-hours versus angler-hours is presented below (p. 50).

Yield and Fishing Intensity

Figs. 8-13 show the relationships between yield and fishing intensity for various seasons of the year. Log-log plots of yield in numbers of fish for winter, open-water, and annual periods, have slopes of one, but for spring and summer have slopes of 1.25 and 1.22, respectively (Tables 3 and 4, Figs. 10 and 11). The reason for this is not clear, especially as the same relationship for open-water fisheries, which spans both spring and summer, has a slope not statistically different from one (Table 5, Fig. 12).

The relationships between yield in weight (kg) versus fishing intensity for winter, open-water, and annual periods have slopes less than one, while spring and summer periods have slopes near one (Tables 2-6 and Figs. 8-13). Again, a discrepancy exists between open-water versus spring and summer analyses, possibly due to very low yields in one lake (lake 21). In general, with the above noted exception, yields in weight decline per unit intensity of fishing as fishing intensity increases. The reason for this is probably that the most intensive fisheries occur on small lakes which also tend to produce smaller fish than large lakes. If small lakes produce as many fish per hectare as larger

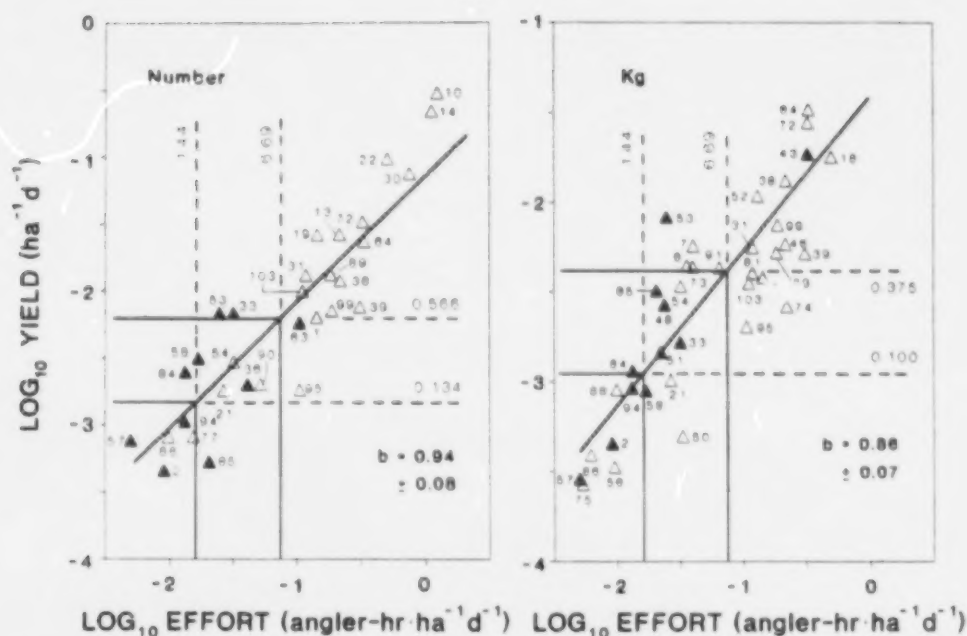


FIG. 8. The relationship between yield in number and kilograms of lake trout and fishing intensity (angler-hours ha⁻¹d⁻¹) during winter. The numbers opposite the symbols refer to lakes described in Appendices A, B, and C. The solid triangles indicate wild, unstocked populations. The solid and dashed horizontal lines correspond to yields of 0.375 (upper) and 0.100 (lower) kg ha⁻¹ for the winter fishing season.

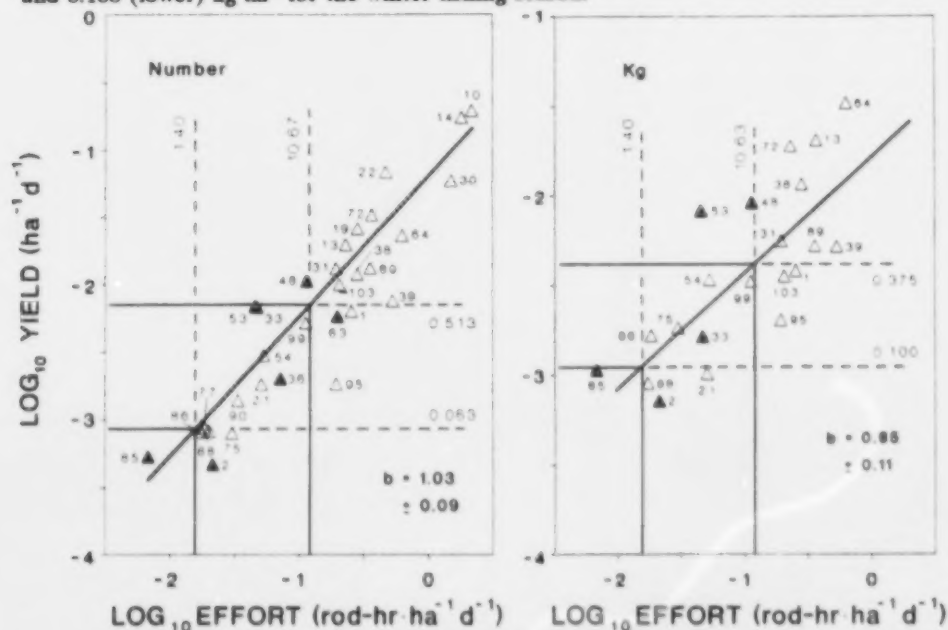


FIG. 9. The relationship between yield in number and kilograms of lake trout and fishing intensity (rod-hours ha⁻¹d⁻¹) during winter. The numbers opposite the symbols refer to lakes described in Appendices A, B, and C. The solid triangles indicate wild, self-sustaining, unstocked populations. The solid and dashed horizontal lines correspond to yields of 0.375 (upper) and 0.100 (lower) kg ha⁻¹ for the winter fishing season.

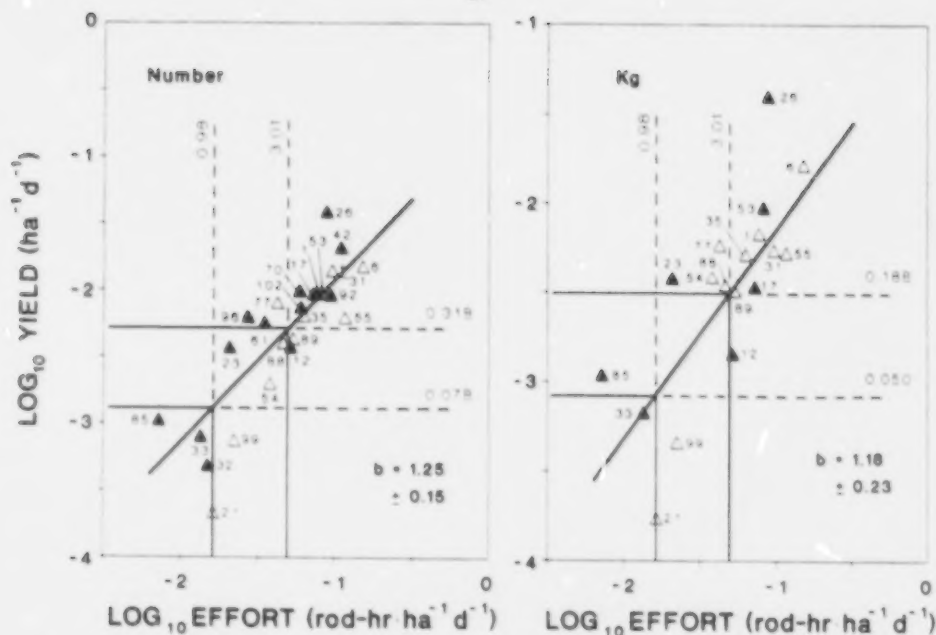


FIG. 10. The relationship between yield in number and kilograms of lake trout and fishing intensity (rod-hours ha⁻¹ d⁻¹) during spring. The numbers opposite the symbols refer to lakes described in Appendices A, B, and C. The solid triangles indicate wild, self-sustaining, unstocked populations. The solid and dashed horizontal lines correspond to yields of 0.1875 (upper) and 0.050 (lower) kg ha⁻¹ for the spring fishing season.

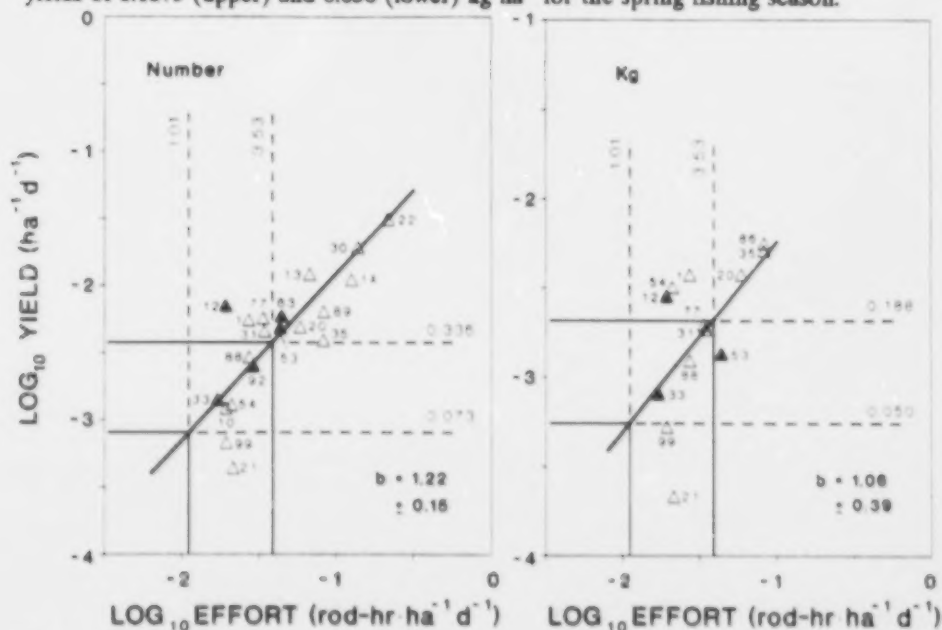


FIG. 11. The relationship between yield in number and kilograms of lake trout and fishing intensity (rod-hours ha⁻¹ d⁻¹) during summer. The numbers opposite the symbols refer to lakes described in Appendices A, B, and C. The solid triangles indicate wild, self-sustaining, unstocked populations. The solid and dashed horizontal lines correspond to yields of 0.1875 (upper) and 0.050 (lower) kg ha⁻¹ for the summer fishing season.

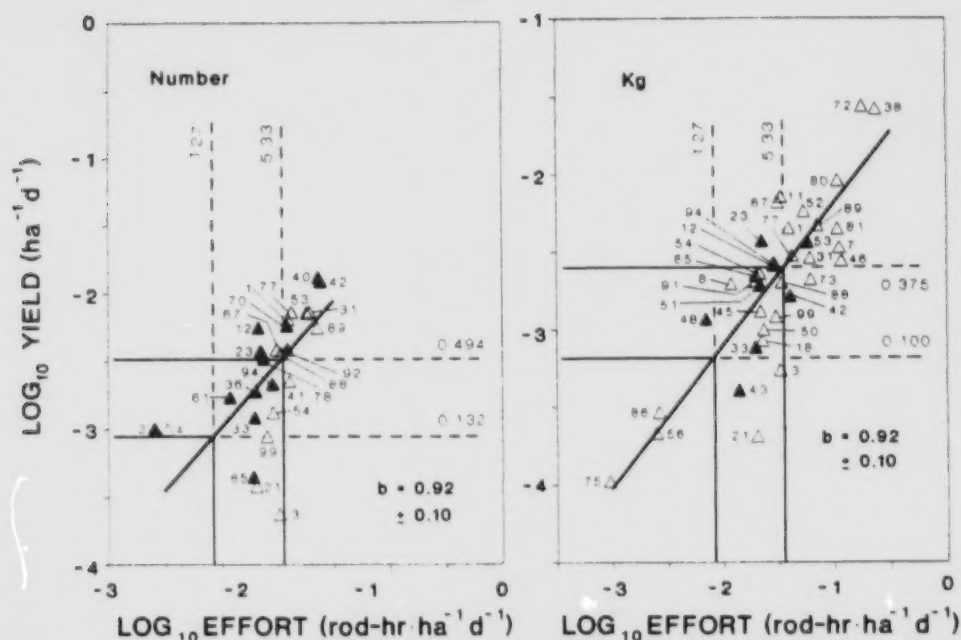


FIG. 12. The relationship between yield in number and kilograms of lake trout and fishing intensity (rod-hours $\text{ha}^{-1} \text{d}^{-1}$) during the open-water fishing season. The numbers opposite the symbols refer to lakes described in Appendices A, B, and C. The solid triangles indicate wild, self-sustaining, unstocked populations. The solid and dashed horizontal lines correspond to yields of 0.375 (upper) and 0.10 (lower) kg ha^{-1} for the open-water fishing season.

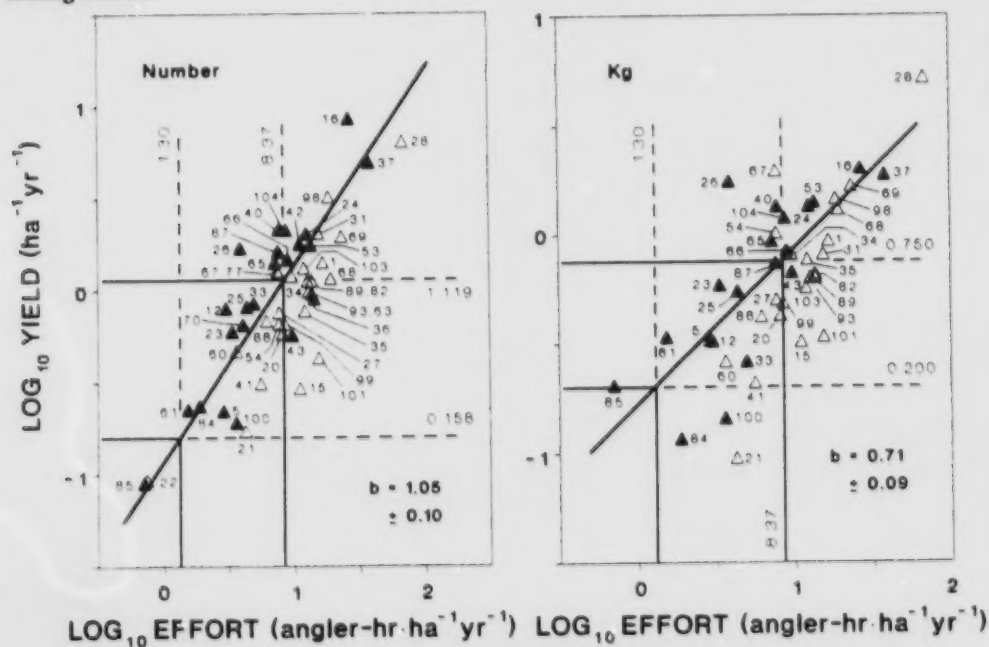


FIG. 13. The relationship between yield in number and kilograms of lake trout and fishing intensity (angler-hours $\text{ha}^{-1} \text{yr}^{-1}$). The numbers opposite the symbols refer to lakes described in Appendices A, B, and C. The solid triangles indicate wild, self-sustaining, unstocked populations. The solid and dashed horizontal lines correspond to yields of 0.75 (upper) and 0.20 (lower) $\text{kg ha}^{-1} \text{yr}^{-1}$.

ones at comparable effort, which seems to be the case in that log yield and log fishing intensity are linearly related with slopes near unity, one would expect yield in weight to decline at the highest fishing intensities, because the greatest fishing intensity occurs in the smallest lakes (Tables 8-12), which also tend to produce smaller fish (Payne et al. 1990).

The reason that small lakes produce smaller fish is not obvious. Two possible reasons are: (1) that small lakes do not provide the physical space required for maximum growth of large fish; lake volume increases as a power function of lake area with an exponent greater than one, therefore, relatively more volume is available in large lakes, especially for mid-water prey species, such as lake herring (*Coregonus artedii*), that use the entire water column and, as a prey species, produce excellent growth in lake trout (Martin 1970); and (2) that compensatory population changes that occur at high rates of exploitation-induced mortality cause yield in weight of fish per unit effort and mean body weight to decline as effort increases, fishing intensity generally being highest in small lakes. It is not possible to determine which of these explanations accounts for the present observations. Possibly both factors are operating. If compensation in numbers and weight occurs under exploitation as described, however, it is clear that yield in weight will be a more sensitive indicator of excessive exploitation than numbers of fish harvested, because numbers of fish will increase as average body size and age decline with increasing exploitation, while biomass will decline as the theoretical MSY is surpassed. Yield in weight, therefore, would be expected to show the earliest decline per unit effort as fishing intensity increases.

Plots of yield versus fishing intensity (Figs. 8-13) and their regressions provide representations of relative performance among lake trout fisheries. Yields and fishing intensities for individual lakes are indicated on each of the seasonal scatter plots (Figs. 8-12) and for the annual plot (Fig. 13). Numbers adjacent to the data points correspond to lakes listed in Appendices A, B, C, and D. Deviations from the fitted regressions of yield versus fishing intensity indicate lakes producing either more than (positive deviations) or less than (negative deviations) the least squares determined norm. Negative deviations, if large, might indicate a naturally unproductive or possibly a stressed population. These plots provide a basis for comparing the relative performances of lake trout lakes, and indicate the range and variation of fishing intensities and yields observed in Ontario lake trout lakes. Hence, they provide a quantitative basis for diagnosis of potential problems.

Relative Exploitation Levels Among Lakes

Martin and Olver (1980) reported that many lakes with self-sustaining lake trout populations are capable of sustained annual yields of 0.25-0.75 kg ha⁻¹. Healey (1978) stated, however, that sustainable yields of lake trout are unlikely to exceed 0.5 kg ha⁻¹yr⁻¹. His assessment was based on analysis of empirical data on population density, productivity, and mortality rates. The estimated yield for the Lake Opeongo lake trout population for the period 1965-79 is about 0.68 kg ha⁻¹yr⁻¹ (Payne et al. 1990). The Opeongo population has sustained yields in this range for many years, but is now approaching, or may have passed, the threshold of excessive exploitation, given present maturity and fishing vulnerability schedules (Matuszek et al. 1990).

Long-term yields of lake trout in the present lake set vary from 0.2 to >3.0 kg ha⁻¹yr⁻¹, primarily due to variation in the quantity and quality of the habitat and lake productivity and, in some cases, artificial recruitment (stocking) (Martin and Olver 1980; Payne et al. 1990). If we accept lake trout yields within the range 0.2-0.75 kg ha⁻¹yr⁻¹, as generally representative of moderate, relatively safe yields, we can readily categorize the levels of exploitation for lakes in the data set. As total annual harvest is partitioned roughly equally between the winter and open-water fisheries, we have set acceptable harvests for these fisheries at 0.10-0.375 kg ha⁻¹ (i.e. one half the annual rate). Yields of 0.10 and 0.375 kg ha⁻¹ for a 90 d winter fishery would correspond to harvests of 0.0011 and 0.0041 kg ha⁻¹d⁻¹ and fishing intensities of 0.158 and 0.825 h ha⁻¹d⁻¹, or 1.44 and 6.69 h ha⁻¹ for the whole winter season, respectively (Fig. 8). The corresponding limits are given for fishing intensity in rod-hours in Fig. 9. Similarly, yields of 0.10 and 0.375 kg ha⁻¹ for a 153 open-water season correspond to 0.0007 and 0.0025 kg ha⁻¹d⁻¹ and fishing intensities of 0.0083 and 0.0349 h ha⁻¹d⁻¹, or 1.27 and 5.33 h ha⁻¹ for the open-water season, respectively (Fig. 12). In the same way, harvests during spring and summer contribute approximately equally to the open-water harvest, therefore, acceptable harvests during those seasons would be 0.050-0.1875 kg ha⁻¹. These limits have been plotted for spring and summer yield data (Figs. 10 and 11), revealing similar ranges of acceptable fishing intensities for these two seasons (spring: 1.0-3.0 h ha⁻¹; summer: 1.0-3.5 h ha⁻¹).

Annual yield limits of 0.20-0.75 kg ha⁻¹yr⁻¹ have been similarly superimposed on the plots of annual yield versus fishing intensity (Fig. 13). The acceptable range of annual yields corresponds to annual fishing intensities of 1.30-8.37 h ha⁻¹yr⁻¹.

Risk of Overexploitation

We define overexploitation as a rate of fishing and fish removal that causes changes in the abundance of mature fish sufficient to lower the natural productive capacity below that required to achieve optimum yield. Yields for lakes in our data set, in most cases, represent point-in-time rather than sustained yields, although in some cases as noted earlier, the reported values are averages over several years. The ranges of acceptable yields for the annual and seasonal data in Figs. 8-13, however, are for sustained yields. The zones delimited by the boundaries represent low, moderate, and high rates of either yield or fishing intensity. Each combination of fishing intensity and yield, therefore, can be associated with the degree of concern about possible overexploitation (Fig. 14).

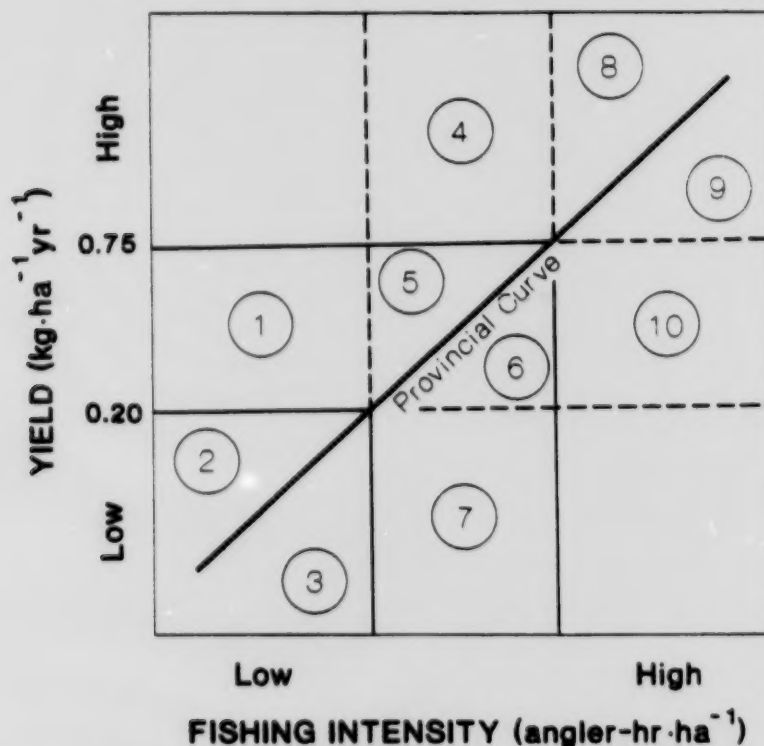


FIG. 14. Diagrammatic plot of yield in kilograms and fishing intensity with zones of low, moderate and high yields indicated by boundaries at 0.20 and 0.75 kg ha⁻¹ yr⁻¹. Levels of fishing and yield demarcated by these values are associated with varying degrees of concern about overexploitation on an arbitrary scale from 1 to 10. Degrees of concern are as follows: 1 very low; 2 very low; 3 low; 4 low; 5 moderate; 6 moderate; 7 high; 8 high; 9 very high; and 10 very high. This plot provides a reference for comparison of yields among lakes as in Fig. 8-13.

Lakes at fixed fishing intensities, within each of the three levels of fishing shown in Fig. 14, will vary in yield from low to high, as indicated by their deviations from the least-squares regressions for each season (Appendix D). Depending on their productivity and size, lake trout populations will have varying capacities to tolerate fishing (Payne et al. 1980). The risk of overexploitation will be a function, therefore, of the inherent productivity of a given lake and the level of fishing intensity. One population, for example, could be at relatively high risk even at a relatively low fishing intensity, whereas another population could be at a relatively low risk even though fishing intensity might be relatively high. In general, however, we would expect the probability or risk of overexploitation to be highest for lakes having low productivity and to increase as fishing intensity increases. Figure 14 presents a comparative context for evaluating the exploitation status in terms of degrees of concern. Populations having large negative deviations at high fishing intensities would raise the greatest concern, while large positive deviations at low fishing intensity would raise the least concern. Collectively, populations subject to high fishing intensity, therefore, would have a relatively high risk of being overexploited and vice versa. The least-squares regression line for each season, thus provides a provincial reference by which to judge the exploitation status of a given lake trout population (Fig. 14). This information alone, of course, is not adequate to fully diagnose the status of an exploited stock. Once fishing intensity and yield have been assessed, more detailed analyses (e.g. Payne et al. 1990) can be initiated, where needed, to determine vital population parameters (e.g. age structure, mortality rates, recruitment success) and actual population status.

Relationship Between Fishing Intensity and Harvest-per-unit-effort (HUE)

Theoretically, yield increases with fishing intensity to some maximum sustained value, equivalent to MSY, but at even higher levels of effort yield declines. The Schaefer effort-yield model (Ricker 1975, p. 325) describing this phenomenon can be expressed as a polynomial as follows:

$$Y = a \frac{E}{A} - b \frac{E^2}{A^2} \quad [1]$$

where Y is yield; E is fishing effort; A is lake area; E/A is fishing intensity (h ha^{-1}); and a and b are fitted constants. This expression becomes linear for any given production system when transformed to HUE as follows:

$$H/E = a - b \frac{E}{A} \quad [2]$$

where H is harvest in number or kg of fish; and H/E is HUE.

HUE in both number and weight of fish plotted versus fishing intensities for winter, spring, summer, open-water and annual fisheries revealed extremely scattered relationships, but which nevertheless can be interpreted within the context of the above theory. Annual HUE data expressed in number of fish plotted versus fishing intensity (Fig. 15) reveals the same general pattern found for other seasons. The upper right boundary, drawn by eye, delimits the approximate maximum yield level for lake trout in Ontario. The actual slope of the curves is uncertain, but the negative relationship is well predicted by equation [2]. Similarly, other lines of negative slope have been drawn by eye to suggest a family of curves associated with lakes of inherently different productivity. The y-intercepts (a in equation [2]) indicate the maximum HUE to be expected for any particular lake type, ranging from >0.4 fish hr^{-1} of fishing in highly productive lakes having excellent habitat for lake trout to <0.1 in lakes of low productivity having marginal habitat. Several categories of population and community status have been identified, to suggest factors that might influence lake trout productivity and, thus, enable logical groupings or planes of productivity to be rationalized.

This type of plot provides an approach for comparison of the relative productivity of lake trout populations, and suggests hypotheses for exploring possible causes of productivity variation among lakes. For example, the distribution of HUE for wild stocks appears to be greater than for other stocks experiencing introductions. Several other features of Fig. 15 are also noteworthy. First, production shifts from the lower left to upper right of the scatter plot, indicating not only lakes that have inherently different production capacities, but also the directions of lake degradation or rehabilitation; the latter being reversible processes. For example, as habitat is lost, production would be expected to shift downward and the HUE versus fishing intensity plot (Fig. 15) would also shift downward and towards the origin. At right angles to the production trajectory is the exploitation trajectory as indicated by the diagonal lines. HUE declines as fishing intensity increases and vice versa, although time lags would probably vary depending on whether fishing was increasing or decreasing. A totally self-regulated fishery would be expected to oscillate backwards and forwards along the exploitation-effort axis, while remaining within bounds defined by the systems productivity

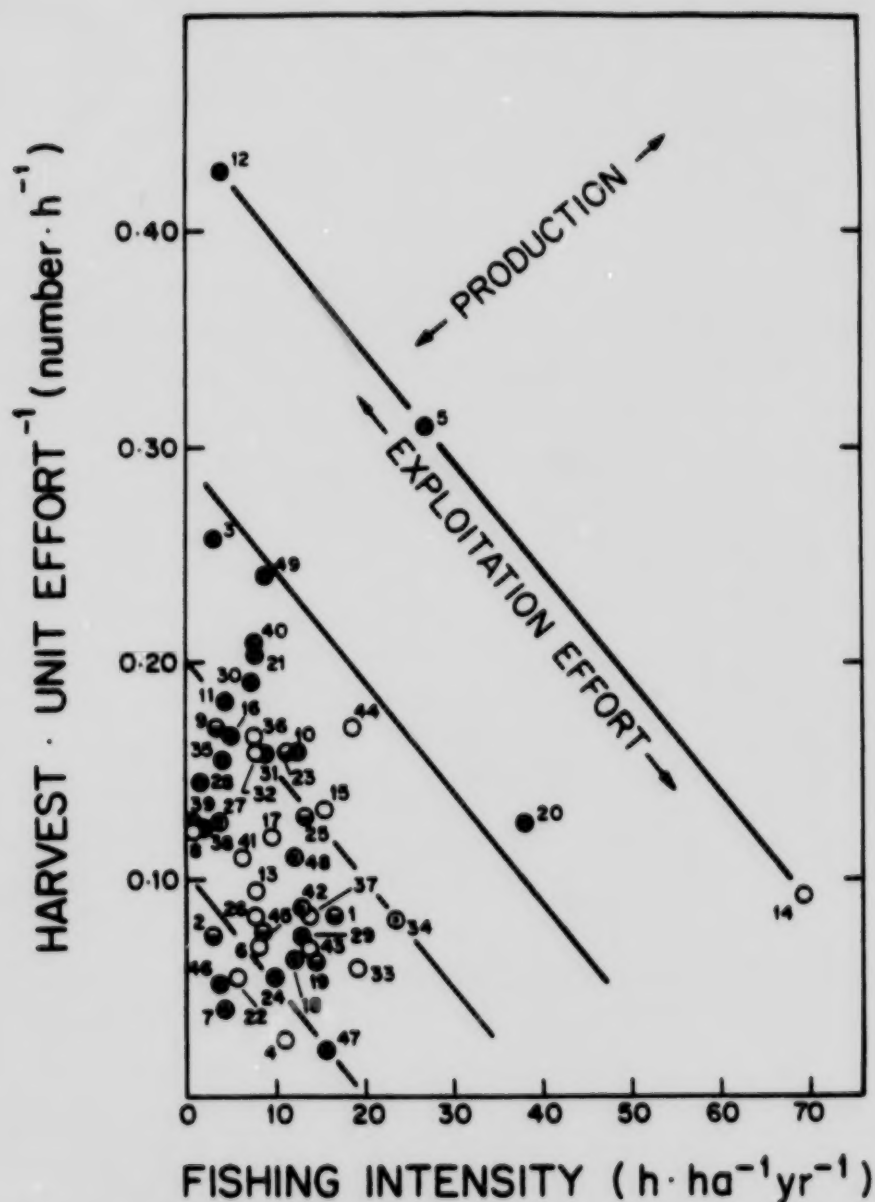


FIG. 15. The relationship between harvest-per-unit-effort (HUE) in number of lake trout per hour and fishing intensity. The diagonal lines have been fitted by visual inspection to suggest various planes of production. Closed symbols indicate wild, self-sustaining lake trout stocks, half closed circles and circles with dots are lakes that had introductions of rainbow smelt (*Osmerus mordax*) and walleye (*Stizostedion vitreum vitreum*). Open circles are lakes that have received some level of lake trout stocking. Opposing arrows along the exploitation-effort axis indicates the reversible effect of fishing intensity on HUE.

and response time, as well as by the sensitivity of the compensatory mechanisms. Compensatory mechanisms of fish populations would operate along the production and exploitation trajectories, because both can influence longevity, population density, and in turn, growth, reproduction, and recruitment rates. As fishing effort increases on a given lake, harvest will increase until a maximum harvest is reached. The harvest maximum represents the maximum surplus harvest on the surplus production plot (Ricker 1975). Therefore, HUE will be maximal on a given lake when exploitation is first initiated and decline as effort increases, reaching some intermediate level at maximum sustainable harvest (see Lester et al. 1991, Fig. 2, p. 6). Beyond MSY, the HUE will continue to decline. MSY and HUE at a given effort will vary, depending on lake productivity.

Fishing intensity causes changes in fishing success and effort ha^{-1} responds to changes in HUE, depending on the expectation of anglers (Goddard et al. 1987). Although we did not evaluate this compensatory response of anglers to fishing success, it is important to note that HUE and fishing effort can have reverse roles as dependent variables, and that both relationships are important components of these fishery systems. Further research will be required to resolve the ways in which these variables interact in lake trout angling fisheries and to interpret observed HUE values for lakes of inherently different productive capabilities.

Effect of Lake Size on Harvest and Yield

Lake size would be expected to affect harvest of lake trout in two possible ways. First is the scale effect in which harvest simply increases as a positive function of lake size. The second effect of lake size is the possible inherent difference in productivity of small versus large lakes (Ryder 1982). Small lakes, for example, having greater shoreline to surface area ratios might be expected to be more productive, because of the importance of the land-water interface for inputs of allochthonous materials and dissolved minerals and nutrients. Also, the ratio of productive littoral benthic zone to lake area will similarly decline as lake area increases. Other arguments, relating to solar insolation and lake area, suggest that small lakes that have larger area to volume ratios than large lakes, would suffer less dissipation of energy, in the form of nutrient and heat loss, to the deeper less productive lake strata (Ryder 1982).

For total fish production in temperate lakes, these relationships appear to hold in that yield is positively correlated with TDS and negatively correlated with mean depth (Youngs and Heimbuch

1982). Lake trout, in contrast, are found in deep, relatively unproductive lakes (Martin and Olver 1976; Johnson et al. 1977). Paradoxically, therefore, greater yields of lake trout might be expected from larger lakes which, in theory, should be inherently less productive. Understanding of the influence of lake size, both on lake trout production and on fishing behaviour, is clearly of importance for management of these systems.

A significant effect of lake area on harvest, independent of fishing effort, was found in only in two cases: for harvest in weight (kg) for annual data (Table 7, Fig. 6); and for harvest in weight during winter, but only when effort is expressed in rod-hours (Table 3, Fig. 2). In these cases, however, area explains only 4% and 10%, respectively, of the total variation in harvest, while effort explains 80% and 71%, respectively. In both cases, where an area effect on total harvest was found, the relationship was positive, larger lakes producing larger total harvests at comparable levels of effort (Fig. 2 and 6).

Area alone exerts a large positive effect on total harvest, larger lakes simply being capable of supporting larger populations and harvests. The slope of the relationship between area and number of fish harvested is 0.68 and 0.74 for winter and open-water fisheries, respectively (Tables 3 and 6), with 35% and 51% of the total variation being explained. Similarly the slopes for harvest in weight are 0.35 and 0.51 for winter and open-water, respectively, but with only 15% and 24% of the variation being explained. The comparable slopes for annual harvests are 0.53 (number of fish) and 0.72 (kg of fish), with 37% and 69% of the variation explained (Table 7). Thus, for the annual estimates, total harvest in weight is more strongly influenced by area than is the number of fish. This result suggests not only more fish in larger lakes, but also bigger fish.

Fishing effort is also positively correlated with lake area, accounting for 22-73% of the variation in effort depending on season (Tables 3-7). Thus, large lakes support more fishing than smaller ones. The question arises, however, whether large and small lakes are equally productive on a per area basis. In general, both fishing intensity and yield are negatively correlated with lake area (Tables 3-7), suggesting that fishing intensity and yield are highest on small lakes. Superficially, this result appears to be consistent with the idea that small lakes are more productive than large lakes, as was suggested by some theoretical considerations noted above (see also Ryder 1982). Several factors could cause yield to decline with increasing lake size, including behaviour of the fishermen; the production of the

lakes; and the effect of stocking, if these factors are differentially expressed for small versus large lakes.

Effort and harvest in small, medium, and large lakes - The harvest data for each season has been summarized for three categories of lake size: <500 ha; 501-2500 ha; and >2501 ha (Tables 8-12). Total catch and effort progressively increases with lake size, but fishing intensity, expressed in hours ha^{-1} , is highest in small lakes and lowest in large lakes (Tables 8-12). For example, during winter, fishing intensity (angler-hours $\text{ha}^{-1}\text{d}^{-1}$) is 6.6 times greater in small lakes than in large lakes (Table 8a). Fishing intensity in winter in rod-hours $\text{ha}^{-1}\text{d}^{-1}$, however, is only 1.78 times greater in small lakes than in large lakes (Table 8b).

Sample sizes are smaller during spring and summer, but some possible differences are worth noting. Fishing intensity during spring is 2.0 times greater in small lakes than in medium size lakes (Table 9), while summer fishing intensity is similar on small and medium size lakes (Table 10). Only two large lakes are present in the summer sample, but they are noteworthy in that they have very high fishing intensity, 3.5 times the geometric mean for the small lakes. This indicates that summer angling for lake trout can be intensive on larger lakes, because of the presence of more tourist facilities, such as lodges, marinas, access points, and cottages.

The pattern of fishing intensity during the entire open-water season is quite similar to that for the winter season, small lakes being about 2-8 times more intensively fished than medium and large lakes, respectively (Table 8a, 11). A similar pattern emerges for effort data summarized over the entire year, fishing intensity in small lakes being 2.6 and 4.6 times greater than in medium and large lakes (Table 12).

In general, total harvests are highest in the large lakes and lowest in the smallest, however, some unexpected variation in yield occurs over lake sizes and seasons. With the exception of the summer season, yield in number of fish is highest in small lakes, varying from 0.25-0.76 fish ha^{-1} over winter, spring, and summer seasons in lakes <500 ha and from 0.31-2.02 fish ha^{-1} in lakes >2501 ha (calculated from Tables 8-10). The medium-size lakes yielded the lowest numbers of fish ha^{-1} during winter, summer, and the open-water period, but sample sizes are low. Data for large lakes were not available for the spring sample and only data for two lakes were available for the summer sample. The latter two lakes had exceptionally high harvests averaging 2.02 fish ha^{-1} . Both of these lakes were

TABLE 8b. Summary of winter angling statistics for lake trout in inland Ontario lakes. Fishing effort is given in rod-hours. Season totals are expressed in units per season.

Lake size (ha)	Statistics	Actual lake area (ha)	Survey duration (d)	Harvest and yield							
				Effort (log ₁₀)		By number of fish (log ₁₀)		By weight (log ₁₀)		HUE (log ₁₀)	
				hr d ⁻¹	hr ha ⁻¹ d ⁻¹	fish d ⁻¹	fish ha ⁻¹ d ⁻¹	kg d ⁻¹	kg ha ⁻¹ d ⁻¹	fish hr ⁻¹	kg hr ⁻¹
				Season totals							
<500	Mean	203	68	1.67	-0.71	0.66	-1.95	0.38	-2.36	-1.24	-1.50
	sd	170	33	0.90	1.02	0.75	1.15	0.26	0.50	0.37	0.35
	# of lakes	39		17	17	17	17	12	12	17	12
	G.M.	174		3,181	13.26	310	0.71	163	0.30	0.058	0.032
501-2500	Mean	1,277	68	1.88	-1.17	0.82	-2.41	0.42	-2.85	-1.19	-1.44
	sd	782	33	1.38	1.43	1.02	1.35	0.08	0.29	0.54	0.41
	# of lakes	24		7	7	7	7	5	5	6	4
	G.M.	1,175		5,158	4.60	449	0.26	178	0.10	0.065	0.036
>2501	Mean	18,670	68	3.07	-0.96	1.93	-2.12	1.58	-2.27	-1.19	-1.05
	sd	49,859	33	0.63	0.93	0.74	1.34	0.46	0.54	0.53	-
	# of lakes	11		6	6	6	6	4	4	6	1
	G.M.	10,000		79,893	7.46	5,787	0.52	2,585	0.37	0.064	-

TABLE 10. Summary of summer angling statistics for lake trout in inland Ontario lakes. Fishing effort is in rod-hours. The percentage of lakes stocked refers to the fraction of lakes in the sample that have been stocked on at least one occasion. Season totals are expressed in units per season.

Lake size (ha)	Statistics	Actual lake area (ha)	Survey duration (d)	Harvest and yield										
				Effort (log ₁₀)		By number of fish (log ₁₀)		By weight (log ₁₀)		HUE (log ₁₀)		Lake trout stocked		
				hr d ⁻¹	hr ha ⁻¹ d ⁻¹	fish d ⁻¹	fish ha ⁻¹ d ⁻¹	kg d ⁻¹	kg ha ⁻¹ d ⁻¹	fish hr ⁻¹	kg hr ⁻¹	number yr ⁻¹	number ha ⁻¹ yr ⁻¹	
														% lakes stocked
<500	Mean sd # of lakes	252 194 13	106 15.4	0.86 0.28 11	-1.47 0.35 11	-0.16 0.39 11	-2.49 0.52 11	-0.40 0.38 8	-2.78 0.39 8	-0.98 0.34 12	-1.22 0.41 9	4,730 9,971 10	16.5 23.2 10	77
				Season totals										
	G.M.	229		768	3.59	73	0.34	42	0.18	0.104	0.060			
501-2500	Mean sd # of lakes	1,043 576 10	106 15.4	1.45 0.53 7	-1.47 0.48 7	0.37 0.66 7	-2.55 0.66 7	0.07 0.52 5	-2.90 0.63 5	-1.23 0.44 9	-1.31 0.10 2	6,136 5,236 8	6.0 3.5 8	80
				Season totals										
	G.M.	1,000		2,987	3.59	248	0.30	125	0.13	0.059	0.049			
>2501	Mean sd # of lakes	3,490 4,701 2	106 15.4	2.68 0.12 2	-0.92 0.51 2	1.87 0.02 2	-1.72 0.41 2			-0.80 0.10 2		19,322 2,595 2	6.5 6.9 2	100
				Season totals										
	G.M.	3,236		50,736	12.74	7,858	2.02							0.157

TABLE 11. Summary of open-water angling statistics for lake trout in inland Ontario lakes. Fishing effort is in rod-hours. Percentage of lakes stocked refers to the fraction of lakes in the sample that have been stocked on at least one occasion. Season totals are expressed in units per season.

Lake size (ha)	Statistics	Actual lake area (ha)	Survey duration (d)	Harvest and yield											
				Effort ($\log_{10}$)			By number of fish ($\log_{10}$)		By weight ($\log_{10}$)		HUE ($\log_{10}$)			Lake trout stocked	
				hr d ⁻¹	hr ha ⁻¹ d ⁻¹	fish d ⁻¹	fish ha ⁻¹ d ⁻¹	kg d ⁻¹	kg ha ⁻¹ d ⁻¹	fish hr ⁻¹	kg hr ⁻¹	number yr ⁻¹	number ha ⁻¹ yr ⁻¹	% lakes stocked	
<500	Mean	245	151	1.17	-1.25	-0.07	-2.46	0.04	-2.38	-1.15	-1.16	3,939	16.0		
	sd	166	14.7	0.45	0.45	0.39	0.55	0.68	0.68	0.81	0.41	7,131	17.6		
	# of lakes	29		17	17	10	10	15	15	22	21	21	72		
				Season totals											
501-2500	G.M.	214		2,233	8.49	129	0.52	165	0.63	0.070	0.069				
	Mean	1,261	151	1.43	-1.60	0.32	-2.71	0.23	-2.84	-0.95	-1.16	4,907	4.7		
	sd	691	14.7	0.43	0.46	0.78	0.81	0.83	0.64	0.55	0.65	4,603	4.2		
	# of lakes	24		21	21	12	12	15	15	13	16	13	54		
				Season totals											
>2501	G.M.	1,148		4,064	3.79	315	0.29	256	0.22	0.112	0.069				
	Mean	7,767	151	1.60	-2.18	1.34	-2.63	0.61	-3.18	-1.06	-0.95	17,847	2.2		
	sd	5,015	14.7	0.91	0.85	0.54	0.28	1.02	0.96	0.35	0.26	56,149	5.6		
	# of lakes	10		9	9	4	4	7	7	5	8	5	5		
				Season totals											
	G.M.	7,244		6,011	1.00	3,304	0.35	615	0.10	0.087	0.113				

TABLE 12. Summary of annual angling statistics for lake trout in inland Ontario lakes. Fishing effort is in angler-hours. The percentage of lakes stocked refers to the fraction of lakes in the sample that have been stocked on at least one occasion. Season totals are expressed in units per season.

Lake size (ha)	Statistics	Actual lake area (ha)	Harvest and yield									
			Effort ($\log_{10}$)				By number of fish ($\log_{10}$)			By weight ($\log_{10}$)		
			h d ⁻¹	h ha ⁻¹ d ⁻¹	fish d ⁻¹	fish ha ⁻¹ d ⁻¹	fish d ⁻¹	fish ha ⁻¹ d ⁻¹	kg d ⁻¹	kg ha ⁻¹ d ⁻¹	HUE (log ₁₀) fish h ⁻¹	HUE (log ₁₀) kg h ⁻¹
<500	Mean	201	3.29	1.12	2.40	0.23	2.17	-0.01	-0.89	-1.11	4,087	17.7
	sd	119	0.72	0.53	0.85	0.79	0.66	0.53	0.58	0.36	7,776	17.4
	# of lakes	29	29	29	29	29	26	26	29	26	17	17
	G.M.	158	1,950	13.18	251	1.69	148	0.98	0.139	0.079		
501-2500	Mean	1,131	3.77	0.71	2.97	-0.09	2.86	-0.22	-0.84	-0.97	6,512	5.8
	sd	659	0.57	0.65	0.78	0.80	0.73	0.65	0.39	0.49	5,050	2.5
	# of lakes	16	16	16	16	16	14	14	16	14	7	7
	G.M.	977	5,888	5.13	933	0.81	724	0.60	0.145	0.1107		
>2501	Mean	4,933	3.93	0.46	2.84	-0.63	3.02	-0.45	-1.09	-0.94	29,064	5.2
	sd	3,945	0.70	0.42	0.83	0.51	0.95	-0.94	0.24	0.29	61,174	7.2
	# of lakes	4	4	4	4	4	3	3	4	3	3	3
	G.M.	4,074	8,511	2.88	692	0.23	1,047	0.35	0.082	0.114		

stocked at a relatively high rate of 6.5 yearling trout ha⁻¹, which might partially explain the high angling activity and harvests. Harvest in weight is not available for either lake.

With one exception (winter rod-hour lakes, Table 8b), yield in weight is greatest in the small lakes, intermediate in the medium size lakes, and lowest in the large lakes. The winter yield in weight is lowest in the medium size lakes (reported in rod-hours), but this appears to be an anomaly due to small sample sizes in the medium and large size categories (Table 8b). The progression from high to low harvest intensity for small to large lakes seen in the "angler-hour" lake set (Table 8a) supports this interpretation.

Annual yield in number of fish varies from 1.69 in lakes <500 ha to 0.81 in lakes from 501-2500 ha, to 0.23 in lakes >2501 ha (Table 12). Yield in weight varies from 0.98 to 0.60 to 0.35 kg ha⁻¹ over the same size classes of lakes, respectively. The mean weight of harvested fish, obtained by dividing HUE in weight by HUE in number of fish, was smallest in lakes <500 ha varying from 0.46 (winter, Table 8a) to 0.99 kg (open water, Table 11), and largest in lakes >2501 ha varying from 0.89 (winter) to 1.39 kg (annual estimates, Table 12).

Effect of lake size on HUE - If production of small lakes is greater than large lakes, as suggested by our observation of higher lake trout yields on small lakes, we would expect HUE to be relatively constant over lakes independent of area, because fishing effort is also positively correlated with fishing success and, therefore, responsive to changes in success rate (Goddard et al. 1987). In theory, anglers might not continue fishing on small lakes, if success rates were lower than on larger lakes. HUE would serve as the indicator that would shift fishing effort from lake to lake and thereby serve to equalize HUE as a function of the inherent productive capacity. HUE in weight was not correlated with lake area for our study lakes during winter, but we found a weak negative relationship between lake area and HUE in numbers of fish for winter fisheries, indicating higher catches-per-unit-of-effort despite greater fishing intensity on small lakes. This was further explored to test whether higher yields in small lakes during winter was due to intensive stocking of small lakes (Tables 8-12). A relatively strong negative relationship for HUE and area was found for unstocked lakes ($r^2 = 0.37$), but the relationship was not significant for stocked lakes, indicating that stocking was not responsible for the area effect on HUE during winter. In contrast, however, positive relationships were found between HUE in weight (kg) and area for open-water and annual harvests of fish, but in all other cases regression coefficients were not statistically different from zero (Table 13).

TABLE 13. Summary of the regression analyses for harvest-per-unit-effort (HUE) in number (n) and weight (kg) of lake trout versus lake area and MEI during various seasons. All HUE values are expressed in catch per-angler-hour.

Season	Variables		# of lakes	Regression statistics				
	Dependent	Independent		a	b	S _b	P	r ²
Winter	log HUE (n)	log area (ha)	59	-0.61	-0.11	0.05	0.03	6
		log MEI	60	-0.75	-0.30	0.12	0.02	7
	log HUE (kg)	log area (ha)	56	-1.33	-0.04	0.06	0.47	ns
		log MEI	51	-1.20	0.04	0.12	0.74	ns
Spring	log HUE (n)	log area (ha)	26	-0.66	-0.13	0.12	0.28	ns
		log MEI	26	-0.82	-0.41	0.21	0.07	ns
	log HUE (kg)	log area (ha)	13	-0.95	-0.10	0.22	0.66	ns
		log MEI	13	-0.89	-0.71	0.51	0.19	ns
Summer	log HUE (n)	log area (ha)	23	-0.51	-0.20	0.12	0.10	ns
		log MEI	23	-0.98	-0.13	0.19	0.50	ns
	log HUE (kg)	log area (ha)	11	-0.94	-0.12	0.28	0.68	ns
		log MEI	11	-1.31	0.15	0.41	0.72	ns
Open-water	log HUE (n)	log area (ha)	42	-1.25	0.08	0.09	0.26	ns
		log MEI	41	-0.85	-0.42	0.15	<0.01	15
	log HUE (kg)	log area (ha)	45	-1.69	0.19	0.07	<0.01	13
		log MEI	37	-1.02	-0.26	0.18	0.16	ns
Annual	log HUE (n)	log area (ha)	49	-0.78	-0.05	0.06	0.48	ns
		log MEI	48	-0.75	-0.27	0.13	0.04	7
	log HUE (kg)	log area (ha)	43	-1.35	0.11	0.05	0.04	8
		log MEI	42	-0.90	-0.37	0.10	<0.01	22

In general, correlations between HUE and area were either weak, accounting for only 5-13% of the total variation, or not significant. Definitive interpretation of these results is not possible at present, given that the lakes in our samples are at various stages of fishing development, some being intensively exploited with fisheries supported by stocking and others being moderately exploited and dependent on natural recruitment alone. Given the generally weak correlation between HUE and area, it is possible that higher yields in small lakes are due to higher productivity for lake trout per unit area in these systems. Lack of correlation between HUE or the morphoedaphic index (MEI), however, for winter, spring, and summer fisheries, and significant negative correlations for open-water

and annual fisheries, suggests that variation in general lake productivity is not a significant determinant of the correlations between lake size and effort or yield of lake trout (Table 13).

Lester et al. (1991) reported that annual HUE (kg) for Bone, Chiblow, Christman, Flack, and Opeongo lakes (MSY lakes) was significantly related to lake area as: $\text{HUE (kg)} = 0.036 \text{ Area}^{0.22}$. Our regression estimates for these same lakes were $a = 0.043$ and $b = 0.16$. The relationship for all lakes for which annual HUE (kg) data was available was: $\text{HUE (kg)} = 0.044 \text{ Area}^{0.11}$. Corresponding estimates for lakes of 100, 1000, and 10,000 ha were; MSY lakes 0.093, 0.127, and 0.201 kg hr⁻¹ (based on our calculated regression coefficients) and all lakes ($N = 43$) 0.074, 0.096, and 0.123 kg hr⁻¹, respectively. The lower estimates for the larger lake set probably reflects a combination of factors, including inherent lower productivity, and possibly degraded habitat and recruitment overfishing on many lakes in this group. Comparison with the MSY lakes provides a reference for the bounds of HUE (kg) at or near MSY for relatively productive, unstressed lake trout populations, but does not reveal the exploitation status of other lakes which are at various stages of fishing development or have inherently different carrying capacities for lake trout.

Effects of Productivity and Habitat on Harvest and Yield

Comparison of harvests and yields among lakes (Figs. 3-6 and 8-13, respectively) reveals variation spanning 2 to 3 orders of magnitude in total, and in excess of one order of magnitude even at fixed fishing intensity within seasons. After variation in fishing effort has been accounted for, lake size accounts for a relatively small additional amount of variation (0-10%, Tables 3-7). Factors other than fishing intensity and lake size, therefore, are responsible for major differences in yields of lake trout between lakes, 20-30% of the variance in harvest during winter, open-water, and annual periods being unaccounted for (Tables 3, 6, and 7).

In theory, the factors that account for the inherent differences in productivity between lake trout lakes are: latitude, including insolation and growing season, primarily as these affect abundance of prey and scope for growth of lake trout; edaphic variables, including nutrients and minerals; and the quantity and quality of available habitat. The latter directly determines the amount of physical space that is hospitable to lake trout, and the metabolic scope for activity of all life stages, scope for activity being related directly to the risk of mortality in a given habitat (Priede 1977, 1985).

Edaphic variables that are commonly reported for lake trout lakes include: TDS; water clarity (secchi depth); and less often, total phosphorus (Tp). Quantitative habitat variables include: mean depth (z); volume of adult habitat or thermal habitat volume (THV) and thermal habitat area (THA), as described by Christie and Regier (1988); and nursery habitat volume (NHV) and nursery habitat area (NHA) corresponding to summer habitats of young-of-the-year (YOY) and older juveniles. We define adult habitat (for the purpose of this analysis) as AHV and AHA, the volume and benthic area, respectively, of the 15-30 m depth stratum. We define NHV and NHA as the lake volume and benthic area, respectively, at depths greater than 30 m.

Qualitative habitat variables include temperature and dissolved oxygen, but these are not evaluated until a later section (p. 73). We have used stepwise multiple regression analysis to evaluate the influence of fishing effort, lake area (scale factor), TDS, and secchi (productivity factors) and z, AHA and NHA, or AHV and NHV (habitat factors) on yields of lake trout in Ontario lakes. MEI (Ryder 1965) was also evaluated as a predictor of lake trout yields.

Fishing intensity was the primary determinant of lake trout yields among lakes, accounting for 52-89% of the variation for the various seasonal fisheries, but TDS and the amount of juvenile habitat (NHV) combined to account for an additional 11-20% of the remaining variance in annual yields (Table 14). These variables each accounted for a similar amount of variance, but TDS was negatively correlated with yield, while NHV had a positive effect. Mean depth, AHA, and AHV did not reach the critical 0.15 significance level during any season, and secchi depth reached the 0.10 significance level only for yield in number of fish for the annual data set (Table 14).

The morphoedaphic index (MEI) was *negatively* correlated with total harvest in number, but not for harvest in weight during the open-water season when tested in a stepwise multiple regression with total effort and lake area as covariates. The total variation explained was 76%; effort explaining 68%, MEI explaining 8% and area being insignificant at $P = 0.05$. Yield (fish ha⁻¹) during the open-water season was also similarly correlated with fishing intensity and MEI, 54% of the total variation in harvest being explained. In this case, effort explained 40% and MEI explained 14%. Also, during the open-water season, MEI was negatively correlated with HUE expressed in number of fish, explaining 15% of the total variation (Table 13).

TABLE 14. Summary of stepwise multiple regression analysis of the relationships between yield and fishing intensity, TDS, secchi depth, mean lake depth, and relative amounts of adult habitat (AHA/area; AHV/volume) and juvenile habitat (NHA/area; NHV/volume) for winter, open-water and annual fisheries. Habitat area ratios and habitat volume ratios were tested in separate analyses. Variables were entered and retained in the model only if $P < 0.15$. Statistics for effort, TDS and secchi are given for runs with AHA and NHA only.

Season	Yield	Statistic	Effort h ha ⁻¹	TDS mg l ⁻¹	Secchi (m)	Mean depth	AHA ratio	NHA ratio	AHV ratio	NHV ratio
Winter	No. of fish	b	1.199	-0.435	ns	ns	ns	0.365	ns	0.258
		S _b	0.076	0.176				0.060		0.040
		P	<0.001	0.023				<0.001		<0.001
		r ²	0.803	0.021				0.109		0.112
	Weight (kg)	b	0.959	ns	ns	ns	ns	0.119	ns	0.089
		S _b	0.066					0.057		0.040
		P	<0.001					0.048		0.038
		r ²	0.889					0.018		0.019
Open- water	No. or fish	b	0.818	-0.565	ns	ns	ns	0.176	ns	0.119
		S _b	0.216	0.338				0.091		0.067
		P	<0.002	0.115				0.109		0.135
		r ²	0.421	0.079				0.088		0.078
	Weight (kg)	b	1.015	ns	ns	ns	ns	0.165	ns	0.123
		S _b	0.103					0.080		0.057
		P	<0.001					0.054		0.045
		r ²	0.793					0.036		0.038
Annual	No. of fish	b	0.950	-0.686	-0.601	ns	ns	0.340	ns	0.379
		S _b	0.134	0.209	0.353			1.107		0.109
		P	<0.001	0.014	0.099			0.069		0.067
		r ²	0.527	0.077	0.025			0.038		0.038
	Weight (kg)	b	0.794	-0.458	ns	ns	ns	0.246	ns	0.230
		S _b	0.115	0.164				0.078		0.079
		P	<0.001	0.010				0.009		0.001
		r ²	0.522	0.099				0.083		0.101

MEI was also negatively correlated with total harvest in both number and weight of fish for annual harvest estimates when tested as a covariate with total effort, effort explaining 76% and 84% of the total variance in numbers and weight, respectively. In these cases, MEI explained 3% and 6% of the total variance, respectively, and the effect of area was insignificant. Fishing intensity and MEI combined, also explained 67% and 61% of the variation in annual yield expressed in number and

weight of fish, respectively. Again, MEI was negatively correlated with yield and explained 4% and 9% of the variation, respectively. MEI was also negatively correlated with annual estimates for HUE expressed in both number and weight of fish, MEI accounting for 7% and 22% of the variation in HUE, respectively (Table 13). Independent multiple regression analyses (Table 14) suggest that TDS (rather than mean depth) accounts for the significant effect of MEI.

MEI has been widely used as an estimator of total fish yield (Schlesinger and Regier 1982; Ryder 1982), although recent attempts have been made to partition MEI yield estimates by species (OMNR 1982). In general, MEI has been found to be positively correlated with fish yields (Ryder et al. 1974), but in cases where significant relationships were found, lake trout harvests were always negatively correlated with MEI (Table 13). Ontario lake trout lakes would appear to meet the criteria of homogeneity proposed for application of the MEI yield estimator (Ryder et al. 1974; Ryder 1982), the lakes being located within a relatively narrow latitudinal range and being inhabited by similar fish communities. However, MEI is not a strong predictor of lake trout yields for the present lakes.

Seasonal Variation in Lake Trout Harvests

We examined harvest statistics for lake trout angling fisheries in various seasons of the year, to assess whether a similar amount of effort is expended in each season; whether effort-harvest relationships are similar between seasons; and whether total harvests vary between seasons. Seasonal harvest statistics are summarized in Table 15. The effort and harvest data have been adjusted to correspond to a standard survey day. Geometric means are also given for effort and harvest statistics, but these do not correspond to exactly the same lake sets within each season, because the same observations were not always obtained during each survey. Effort and HUE estimates for winter are given in angler and rod-hours. In all other seasons, angler and rod-hours are equivalent, because only one rod can be legally employed by an angler at a given time during open-water seasons.

Fishing intensity was greater during winter than during either spring or summer, total winter fishing intensity (8.76 rod-hours ha^{-1}) being 4.79- and 2.13-times the spring and summer efforts, respectively (Table 15), although lake areas were not the same between seasons. Total winter effort in rod-hours exceeded by 2.6-fold the spring and summer effort combined. In terms of angler-hours, winter effort ha^{-1} exceeded open-water effort by only a factor of 1.25. Applying equations in Tables 3 and 6, fishing intensity during winter in angler-hours exceeded fishing intensity during the open-water season by 1.28-times, when compared at a common lake size of 1000 ha (Table 15).

TABLE 15. Summary of seasonal harvest and effort data for lake trout fisheries in inland Ontario lakes. Effort and harvest statistics have been standardized to correspond to a survey day and transformed ($\log_{10}$) daily means are reported. The geometric means (G.M.), which are the antilogs of the daily means times the survey duration, represent an estimate of the season totals. Estimates for winter given in angler-hours and rod-hours are not for the identical lakes, although considerable overlap exists.

Harvest and yield														
Lake size (ha)	Survey duration (d)	Actual lake area (ha)	Effort ($\log_{10}$)		By number of fish ($\log_{10}$)		By weight ($\log_{10}$)		HUE ($\log_{10}$)		Lake trout stocked			
			h d ⁻¹	h ha ⁻¹ d ⁻¹	fish d ⁻¹	fish ha ⁻¹ d ⁻¹	fish d ⁻¹	kg d ⁻¹	kg ha ⁻¹ d ⁻¹	fish h ⁻¹	kg h ⁻¹	number yr ⁻¹	number ha ⁻¹ yr ⁻¹	% lakes stocked
<u>Winter - Angler-hours</u>														
Mean	86	2,740	1.72	-1.27	0.51	-2.34	0.49	-2.52	-0.91	-1.21		9,706	10.4	
sd	16.5	9,107	0.94	0.97	1.06	0.89	0.79	0.95	0.45	0.47		33,804	18.0	
# of lakes		74	47	47	31	31	37	37	60	56		55	55	74
Seasonal totals														
G.M.		550	4,513	4.62	278	0.39	266	0.26	0.124	0.062				
<u>Winter - Rod-hours</u>														
Mean	68	2,740	2.01	-0.89	0.80	-2.11	0.29	-2.48	-1.21	-1.47				
sd	33	9,107	1.34	1.12	1.43	1.23	0.08	0.55	0.43	0.36				
# of lakes		74	30	30	30	30	21	21	29	17				
Season totals														
G.M.		550	6,958	8.76	429	0.53	132	0.23	0.062	0.034				
<u>Spring - Rod-hours</u>														
Mean	46	482	1.24	-1.40	0.23	-2.42	-0.13	-2.67	-1.01	-1.20		5,878	17.4	
sd	11.9	637	0.59	0.54	0.74	0.77	0.59	0.73	0.44	0.49		8,638	21.6	
# of lakes		27	25	25	25	25	18	18	26	13		14	14	52
Season totals														
G.M.		316	799	1.83	78	0.17	34	0.098	0.097	0.063				

TABLE 15. Continued

Lake size (ha)	Survey duration (d)	Actual lake area (ha)	Harvest and yield											
			Effort (log ₁₀)		By number of fish (log ₁₀)		By weight (log ₁₀)		HUE (log ₁₀)		Lake trout stocked		% lakes stocked	
			h d ⁻¹	h ha ⁻¹ d ⁻¹	fish d ⁻¹	fish ha ⁻¹ d ⁻¹	kg d ⁻¹	kg ha ⁻¹ d ⁻¹	fish h ⁻¹	kg h ⁻¹	number yr ⁻¹	number ha ⁻¹ yr ⁻¹		
<u>Summer - Rod-hours</u>														
Mean	106	1,009	1.25	-1.41	0.23	-2.44	-0.23	-2.82	-1.06	-1.25	7,337	11.1		
sd	15.4	2,108	0.88	0.46	0.99	0.64	0.52	0.47	0.41	0.37	12,136	19.0		
# of lakes		25	20	20	20	20	13	13	23	11	20	20	80	
Season totals														
G.M.		575	1,885	4.12	180	0.38	62	0.16	0.087	0.057				
<u>Open-water - Rod-hours</u>														
Mean	151	2,195	1.39	-1.61	0.34	-2.54	0.26	-2.78	-1.07	-1.10	7,295	9.8		
sd	14.7	4,853	0.60	0.75	0.80	0.58	0.86	0.85	0.69	0.51	21,884	17.6		
# of lakes		63	47	47	26	26	37	37	40	45	45	39	3962	
Season totals														
G.M.		741	3,707	3.71	338	0.44	275	0.25	0.089	0.079				
<u>Annual - Angler-hours</u>														
Harvest rates per year														
Mean		891	3.51	0.92	2.63	0.04	2.49	-0.12	-0.89	-1.05	9,685	12.7		
sd		1,669	0.83	0.72	0.96	0.93	0.99	0.63	0.51	0.42	26,059	17.9		
# of lakes		49	49	49	49	43	43	49	43	27	27	27		
Season totals														
G.M.		372	3,236	8.32	427	1.10	309	0.76	0.129	0.090				

Total harvest and yield during winter also exceeded harvest during spring and summer both in number and weight of fish taken (Table 15). HUE during winter in number of fish per angler-hour was 1.28- and 1.42-times higher than during spring and summer, respectively, but HUE (angler-hours) in weight was similar in all three seasons (Table 15), indicating that smaller fish were taken during winter. Total harvest and yield in both number and weight of fish was similar between winter and open water, even though the latter season is 68% longer.

The seasonal regression statistics for fishing intensity and yield (numbers and weight) and lake area (Tables 2-6) are summarized with estimates for lakes of 100, 1000, and 10,000 ha in Table 16, to allow direct comparisons of effort and yield. The estimates are not based on the same lakes in each season. Total estimated fishing intensity was similar to slightly higher during winter (16.0 h ha^{-1} for a 100 ha lake, 1.7 h ha^{-1} for a 10,000 ha lake) compared to the open-water season (14.6 and 1.40 h ha^{-1} for 100 and 10,000 ha lakes, respectively). Yields followed a similar seasonal pattern as fishing intensity, yields being highest during winter and lower during spring and summer (Table 16). Winter yields were similar to open-water (spring and summer combined) yields.

Comparison (ANCOVA) of the winter and open-water relationships between fishing intensity, yield (kg), and area revealed no differences in slopes, but significantly higher fishing intensity during winter and similar yield in both seasons at common lake sizes.

Estimated yields in small lakes (100 ha) were about an order of magnitude greater than in large lakes (10,000 ha) during winter, spring, summer, and the combined open-water season. The annual estimates, however, indicated a 2.0 fold difference between yields (kg) for lakes of 100 versus 10,000 ha (Table 16). With reference to our earlier yield guideline of $0.20\text{--}0.75 \text{ kg ha}^{-1}\text{yr}^{-1}$, estimated average yields for small lakes (100 ha) in our lake sets are well in excess of the upper limit (i.e. $0.75 \text{ kg ha}^{-1}\text{yr}^{-1}$) of the moderate-risk range during both winter and open-water seasons. Estimated average yields for medium to large lakes, however, are within the moderate risk range during all seasons (Table 16). Applying the season durations and x on y predictive equation (Table 16), it is possible to determine the lake area that corresponds to the critical yield ($0.75 \text{ kg ha}^{-1}\text{yr}^{-1}$) threshold between moderate and high risk for the winter fishery. The lake size, at which winter fisheries exceed the critical yield threshold, is 1008 ha (95% confidence interval 694-1463 ha).

TABLE 16. Relationships between lake area and fishing intensity (angler hr ha⁻¹), yield in numbers of fish ha⁻¹, and yield in kg ha⁻¹ for lake trout fisheries in inland Ontario lakes during various seasons of the year. Numbers in brackets are 95% confidence intervals of the estimates. Season duration for spring excludes April because of unfishable ice conditions. The annual data includes all open seasons of the year, which in some cases, excluded the winter season.

Season (duration)	Dependent variables	n	Intercept (log y=log a+b log area)	Slope	r ²	Season estimates of effort and yield (ha ⁻¹ season ⁻¹)		
						Lake area (ha)		
						100	1000	10,000
Winter (90)	Effort (h ha ⁻¹ d ⁻¹)	46	0.22	-0.48	0.23	15.95 (7.82-32.52)	5.23 (3.64-7.51)	1.71 (0.85-3.46)
	Yield 1 (no ha ⁻¹ d ⁻¹)	48	-	ns	-	-	0.75 (0.41-1.35)	-
	Yield 2 (kg ha ⁻¹ d ⁻¹)		-0.81	-0.54	0.22	1.16 (0.46-2.90)	0.34 (0.22-0.51)	0.10 (0.04-0.23)
Spring (61)	Effort	25	-0.33	-0.41	0.30	4.44 (2.70-6.97)	1.69 (1.16-2.46)	0.66 (0.26-1.65)
	Yield 1	25	-1.02	-0.54	0.25	0.49 (0.24-1.00)	0.14 (0.08-0.25)	0.04 (0.01-0.16)
	Yield 2	18	-0.73	-0.76	0.40	0.34 (0.15-0.75)	0.06 (0.03-0.12)	0.01 (0.002-0.06)
Summer (92)	Effort	21	-	ns	-	-	3.00 (1.86-4.84)	-
	Yield 1	21	-	ns	-	-	0.28 (0.15-0.51)	-
	Yield 2	14	-	ns	-	-	0.11 (0.06-0.23)	-
Open-water (153)	Effort	48	-0.07	-0.49	0.32	13.48 (7.52-24.18)	4.36 (3.36-5.65)	1.40 (0.85-2.35)
	Yield 1	48	-	ns	-	-	0.52 (0.39-0.69)	-
	Yield 2	39	-	ns	-	-	0.33 (0.21-0.51)	-
Annual	Effort (h ha ⁻¹ yr ⁻¹)	50	1.89	-0.37	0.42	14.63 (11.13-19.23)	6.30 (5.14-7.73)	2.71 (1.71-4.13)
	Yield 1 (no ha ⁻¹ yr ⁻¹)	50	1.06	-0.38	0.28	1.99 (1.36-2.92)	0.83 (0.62-1.11)	0.35 (0.19-0.62)
	Yield 2 (kg ha ⁻¹ yr ⁻¹)	45	0.33	-0.15	0.08	1.05 (0.73-1.52)	0.74 (0.57-0.96)	0.52 (0.31-0.89)

In summary, winter fisheries take greater numbers and weight of lake trout than either spring or summer fisheries. Yields during winter versus all open-water fisheries combined, however, are quite similar (Table 16), notwithstanding the tendency of open-water fisheries to take larger fish. The weighted (years of data) average weight of fish taken in the winter in all lakes is about 0.5 kg, compared to 0.9 kg in the open-water period, based on HUE in numbers and weight of fish (Table 15). Small lakes, in particular, are subject to higher fishing pressure during winter compared to spring and summer, resulting in correspondingly higher yields during winter in those lakes (Table 16). Again, comparing winter with the entire open-water period, fishing effort, and yields on small lakes tend to be similar (Table 16), even though the open-water season was 153 d versus only 90 d for winter. Annual estimates are only generally consistent with totals for the three primary fishing seasons (winter, spring, and summer), possibly because different lakes are represented within each seasonal data set (Tables 15 and 16). The annual estimates do not take into account whether fisheries operated during each season of the year. Thus, for some lakes, the annual estimates were based on open-water angling only, while in others, all seasons were included. Actual mean annual yields reported in the data base were in the order of 1.10 fish ha⁻¹ (95% C.L. = 0.59 - 2.02) and 0.76 kg ha⁻¹ (95% C.L. = 0.49 - 1.18). Adjusted to a lake size of 100 ha, annual yields were 2.20 fish ha⁻¹ and 1.16 kg ha⁻¹. Similarly, for lakes of 1000 and 10,000 ha, annual harvests were 0.63 and 0.18 fish ha⁻¹, and 0.55 and 0.26 kg ha⁻¹, respectively.

Comparison of harvest-effort relationships during winter, spring, and summer - Pair-wise comparisons of the harvest versus effort and area relationships between winter, spring, and summer seasons were tested using analysis of covariance (ANCOVA). Harvest in numbers of fish and in weight (kg) were compared in separate analyses. All variables were transformed to logarithms. Harvest in number of fish between winter, summer, and spring for effort expressed in *rod-hours* was not significant using a partial sum of squares (SS) (Type III) analysis (Fig. 16). Nor was the same analysis comparing harvest in weight (kg) ($F = 2.96$, $P = 0.063$) (Fig. 16). The adjusted harvest at the common level of effort in *rod-hours*, however, was lowest during winter (number of fish: spring = 0.093, summer = 0.096, winter = 0.052 fish per hour of fishing; harvest in weight: spring = 0.065, summer = 0.056, winter = 0.047 kg per hour of fishing).

Comparisons (ANCOVA) of yields versus fishing intensity in *rod-hours* between seasons revealed significant differences between winter and spring ($F = 6.72$, $P = 0.013$), and winter and summer (F

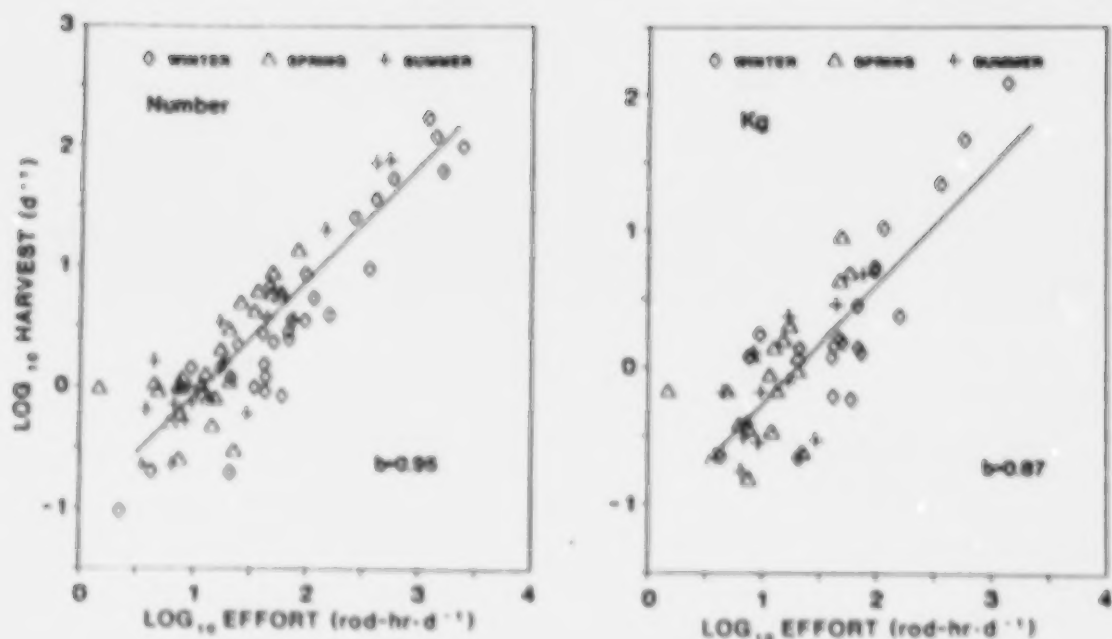


FIG. 16. The relationship between harvest per day in number and weight of lake trout and fishing effort in rod-hours per day for winter, spring, and summer seasons combined.

= 6.91, $P = 0.012$) for harvest in numbers, but neither comparison was significant for harvest in weight (kg). In both cases, however, the adjusted harvests were lower during winter than during spring and summer. None of the seasonal pair-wise comparisons were significantly different when effort was expressed in angler-hours.

The frequency distributions of the seasonal residuals of the pooled harvest versus effort (rod-hours) regressions in numbers and weight of fish illustrate the nature of the seasonal differences (Fig. 17). The distribution of winter residuals in number of fish harvested was positively skewed, while the spring residuals were negatively skewed, and the summer ones were symmetrical. Thus, winter harvests were centered below the common regression line, spring harvests were centered above, and summer harvests were intermediate between winter and spring (Fig. 16). The harvest residuals in weight for winter were well centered on the common regression as were the summer residuals, while the spring residuals were centered above the line. This analysis indicates the tendency of spring fisheries to be more effective per unit effort, in terms of both number and weight of fish harvested. Similarly, winter fisheries were the least effective per unit rod-hour of effort.

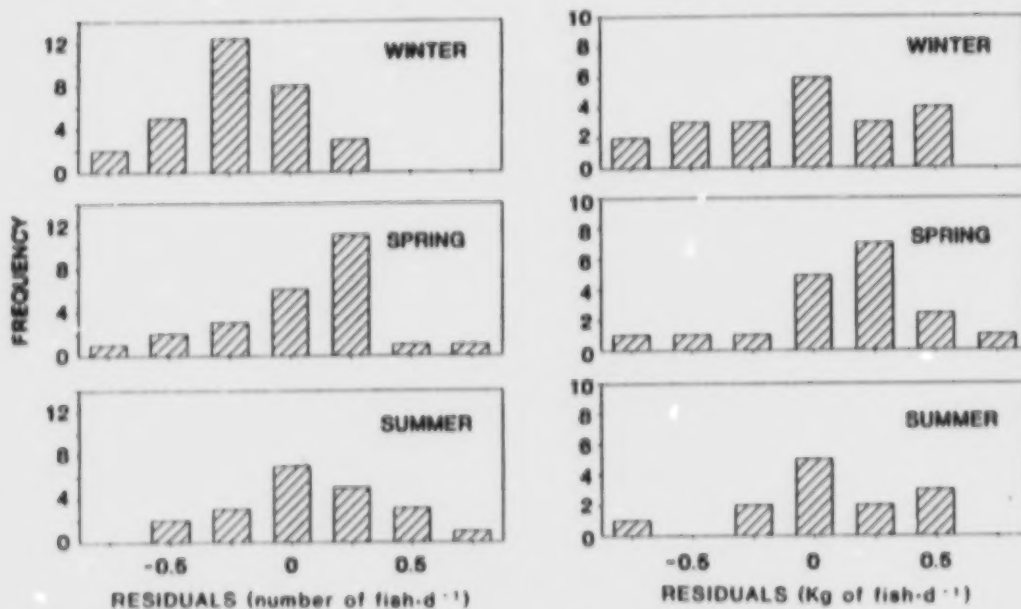


FIG. 17. Frequency distributions of the seasonal residuals of the harvest of lake trout in number and weight and effort regressions in Fig. 16.

No significant differences were found between seasons when effort was expressed in angler-hours (Fig. 18), suggesting that a rod-hour of fishing effort was less efficient during winter than during spring and summer, and that the actual harvest per angler-hour of effort was similar in all seasons because, for the present data sets, the legal use of two lines per angler during winter apparently raises effectiveness during that season to the level attained by open-water anglers.

A similar analysis for the pooled seasonal harvest versus effort in angler-hours (Fig. 18) revealed that the seasonal residuals were relatively symmetrical and well centered on the pooled regression line (Fig. 19). These analyses, taken together, suggest that a rod-hour of fishing effort during winter is not as effective as during open-water seasons of the year. Also, it suggests that the legal use of two lines results in an angler-hour of effort in winter being as effective as during other seasons. Thus, the use of an additional line, which actually results in an average of 1.58 rods per angler (Fig. 7), appears to compensate for the seasonal factors which reduce harvest rates per unit of fishing effort during winter. This conclusion is not inconsistent with Lester et al. (1991), in that, in some cases, use of two rods increased the harvest per angler and, in other cases, actually doubled the harvest over single rod anglers, especially in small lakes.

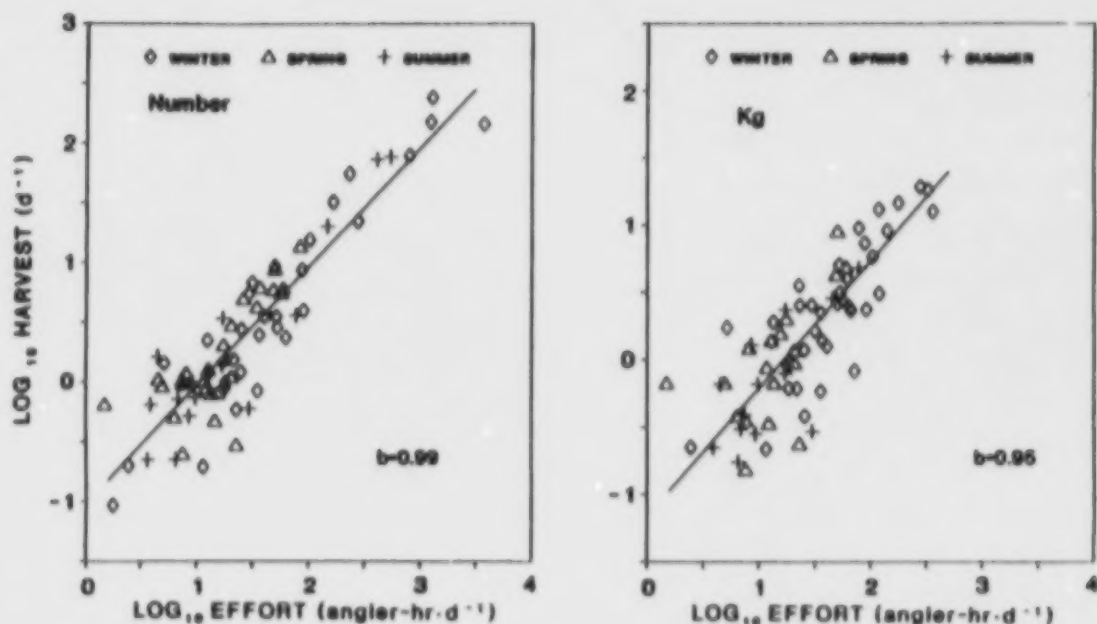


FIG. 18. The relationship between harvest per day in number and weight of lake trout and fishing effort in angler-hours per day for winter, spring, and summer seasons combined.

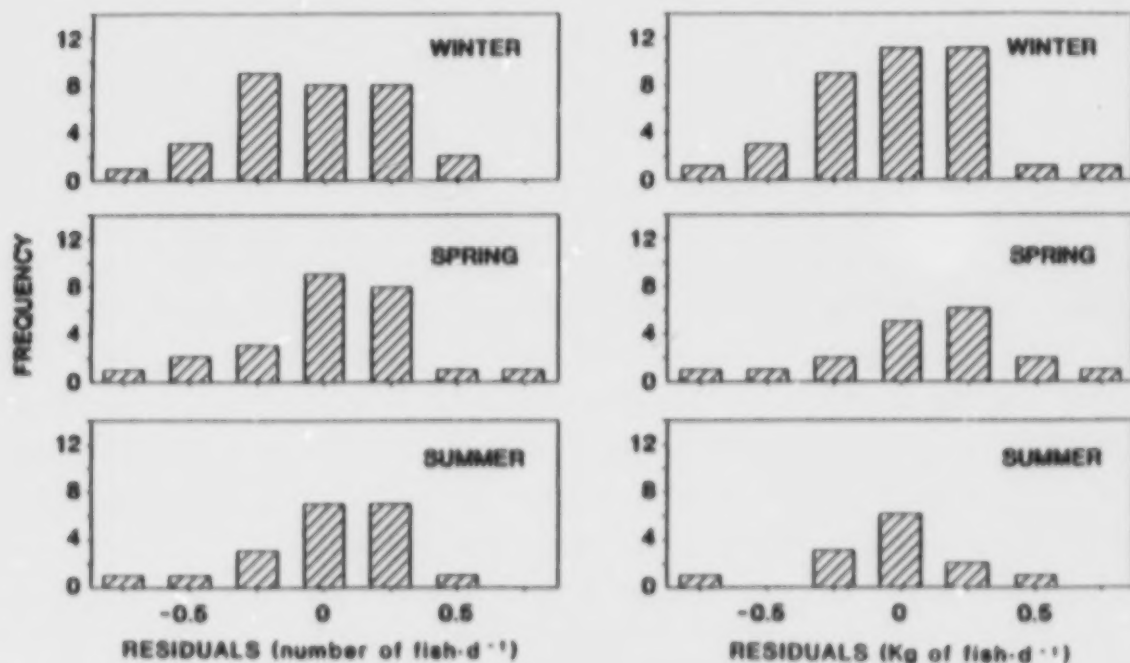


FIG. 19. Frequency distributions of the seasonal residuals of the harvest of lake trout in number and weight and effort regressions in Fig. 18.

Comparison of harvest-effort relationships during winter and open-water seasons - Comparison (ANCOVA) of winter and open-water harvests in weight revealed a similar pattern to that described above, winter harvests being lower, but not significantly so using a Type III SS ($F = 0.59$, $P = 0.448$) when effort was expressed in rod-hours. The adjusted harvests at the common level of effort were: open water = 0.083 and winter = 0.056 kg per rod-hour of fishing (Fig. 20). Harvest in number of fish was not significantly different between winter and open-water fisheries using Type III SS, but the adjusted mean harvest was lower during winter (open-water harvest = 0.068; winter = 0.048 fish per rod-hour of fishing).

The pooled harvest versus effort regressions in *rod-hours* for winter and open-water seasons (Fig. 20) suggested a significant seasonal effect on harvest in weight, but not in harvest in number. A significant area effect was found only for harvest in weight when effort was expressed in *rod-hours* (Fig. 20). The frequency distributions of the winter and open-water residuals from the common regression (Fig. 21) clearly revealed the tendency of winter harvests to be lower at a similar level of effort than open-water harvests; open-water harvests being notably negatively skewed and centered above the pooled regression line (Fig. 20).

The comparable analyses of the pooled harvest versus effort in *angler-hours* indicated that the effort-adjusted harvests are similar between seasons (Fig. 22). The resulting winter and open-water harvest residuals are symmetrical for both numbers and weight of fish harvested and are relatively well centered about the common regression (Fig. 23), indicating no differences between seasons.

Seasonal comparisons using rod-hours versus angler-hours - In an earlier analysis (Fig. 7), we found that an angler-hour of effort during winter is equal to 1.58 rod-hours of fishing effort. Intuitively we would expect the use of an additional fishing line to increase the catch rate of fish. The number of lines used, therefore, needs to be considered in comparing fishing success between seasons. Each additional line, if set at random in a lake, might be expected to increase the probability of capture as a multiple of the probability of capture of a single line. Thus, the theoretical probability of capture of two lines fished in this way would be two times that of one line, and the probability of three lines would be three times that of one line and so on. Fish are not distributed randomly, however, and other factors might also affect fishing success with multiple rods.

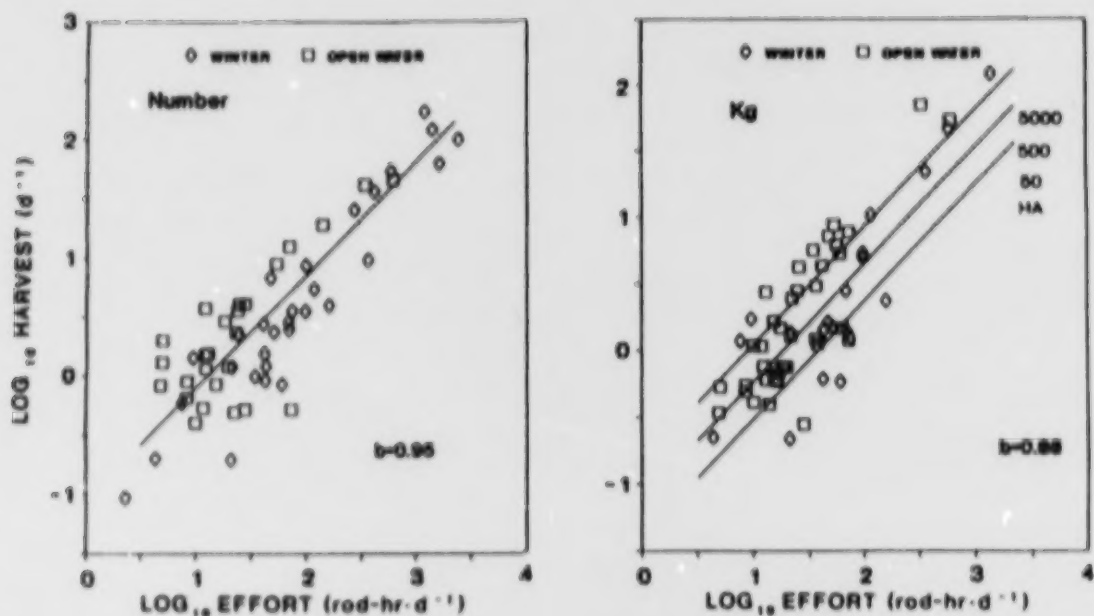


FIG. 20. The relationship between harvest per day in number and weight of lake trout and fishing effort in rod-hours per day for winter and open-water fishing seasons combined.

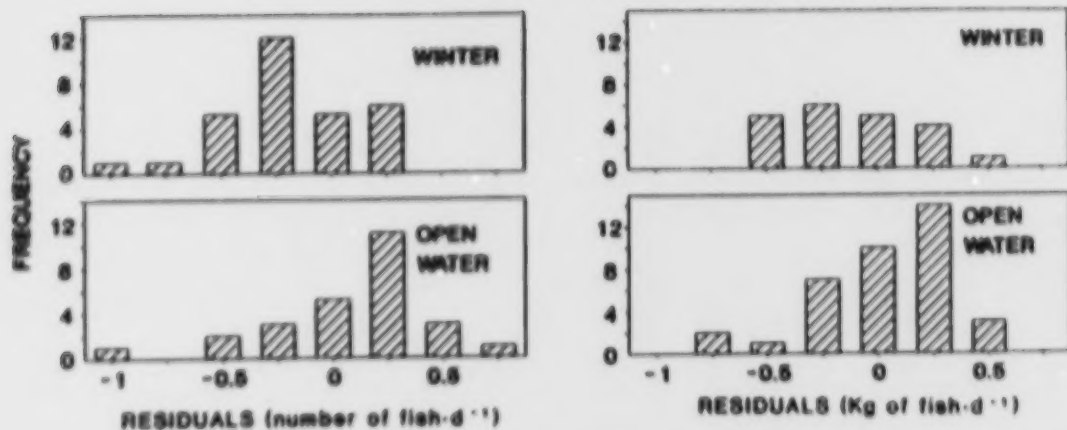


FIG. 21. Frequency distributions of the seasonal residuals of the harvest of lake trout in number and weight and effort regressions in Fig. 20.

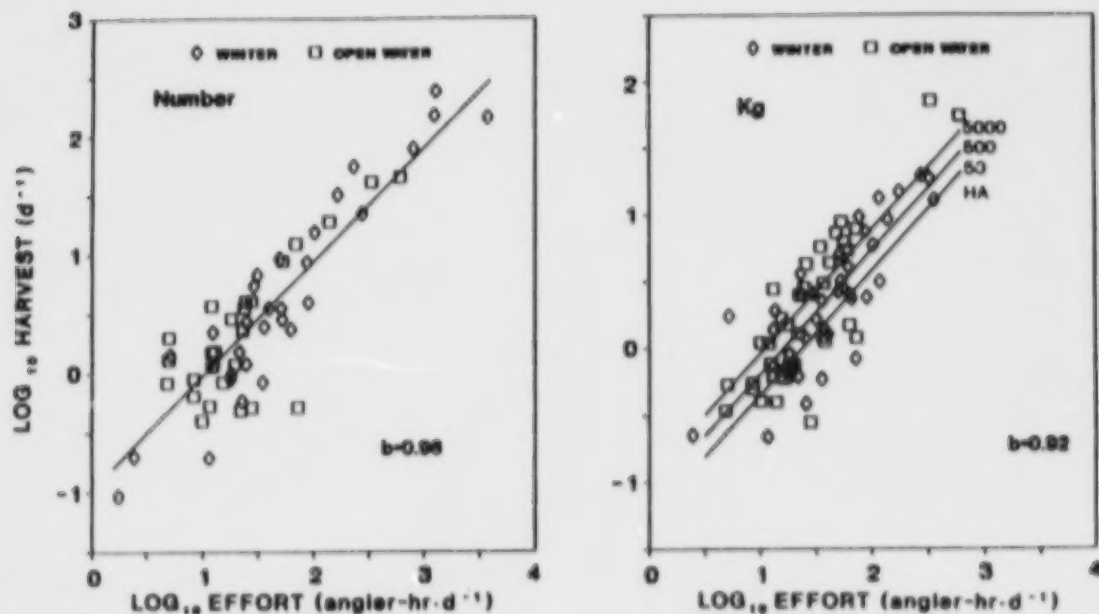


FIG. 22. The relationship between harvest per day in number and weight of lake trout and fishing effort in angler-hours per day for winter and open-water fishing seasons combined.

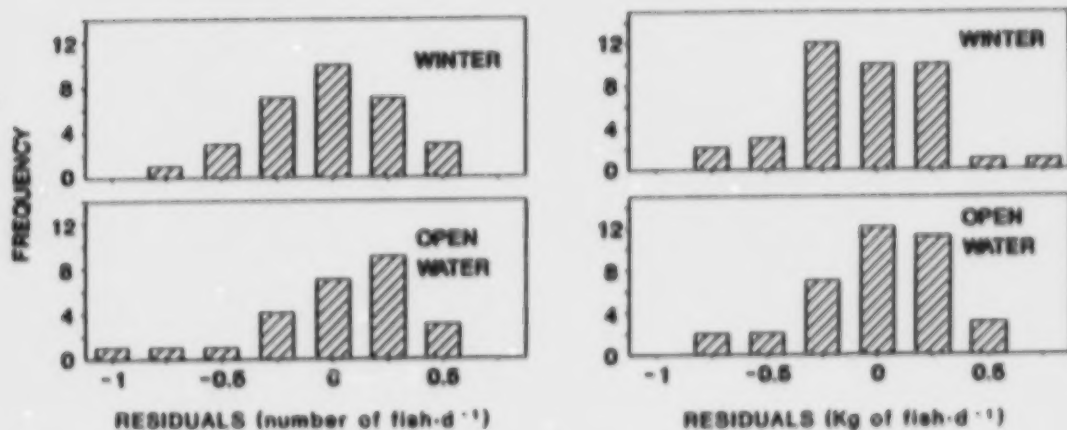


FIG. 23. Frequency distribution of the seasonal residuals of the harvest of lake trout in number and weight and effort regressions in Fig. 22.

The actual effectiveness of each line of a pair operated by an angler, therefore, might be expected to be less than a full unit of effort, because the lines are not set at random and because of the interaction effect between lines that is introduced by the fact that an angler can only attend one line at a time. An attended line might be expected to be more effective than an unattended line. This effect would be expected to reduce the probability of capture to some value less than a full independent unit of effort for each rod of a pair being legally fished during winter. The data necessary to test this hypothesis, however, are not presently available to us. Independent harvest and effort information would be required for anglers using single versus two lines on the same lake at the same time. Lester et al. (1991) have shown that on average for eight lakes, the number of rods (1 versus 2) used by winter anglers did not have a statistically significant effect on catch rate. The observed catch rate in relation to the number of rods used, however, was unpredictable; doubling the number of rods resulted in 0.5- to >2.0-times the catch rate of a single rod. Theoretically, we would expect the effect of two rods per angler to approach the effect of two independent rods in small lakes and to have a lesser effect in large lakes. The reason for this is that fish density and, consequently, encounter rates of stationary baits by randomly swimming fish, would be expected to be highest in small lakes. The analysis by Lester et al. (1991) reveals the effect of two rods to be greatest in the small lakes in their data set. In fact, in 19.4% of the cases examined, doubling the number of rods doubled the catch rate, and this occurred in the small lakes (200-1000 ha). As these authors point out, the effect of two rods requires additional study. For present purposes, we have chosen to report our results in both rod- and angler-hours to avoid imposing premature constraints on the data.

Effort and harvest correlations between seasons - In this section we address the question of predicting effort and harvest for a particular season from effort and harvest estimates in another season for the same lake. The predictive and geometric mean equations of all possible pair-wise seasonal comparisons are provided in Table 17. Significant correlations for fishing effort were found between seasons for winter versus summer (Fig. 24a), open-water (Fig. 24b), and spring (Fig. 25a), and between summer and spring (Fig. 25b). The spring effort, in particular, appears to be well predicted from either winter or summer efforts (Table 17, Fig. 25a, b).

Harvest is less predictable than effort, based on the fisheries in adjacent seasons, with the exception of the spring harvest in both number and weight of fish, which is relatively strongly correlated with summer harvests (Fig. 26 and 27). Neither open-water harvest in number (Fig. 28b)

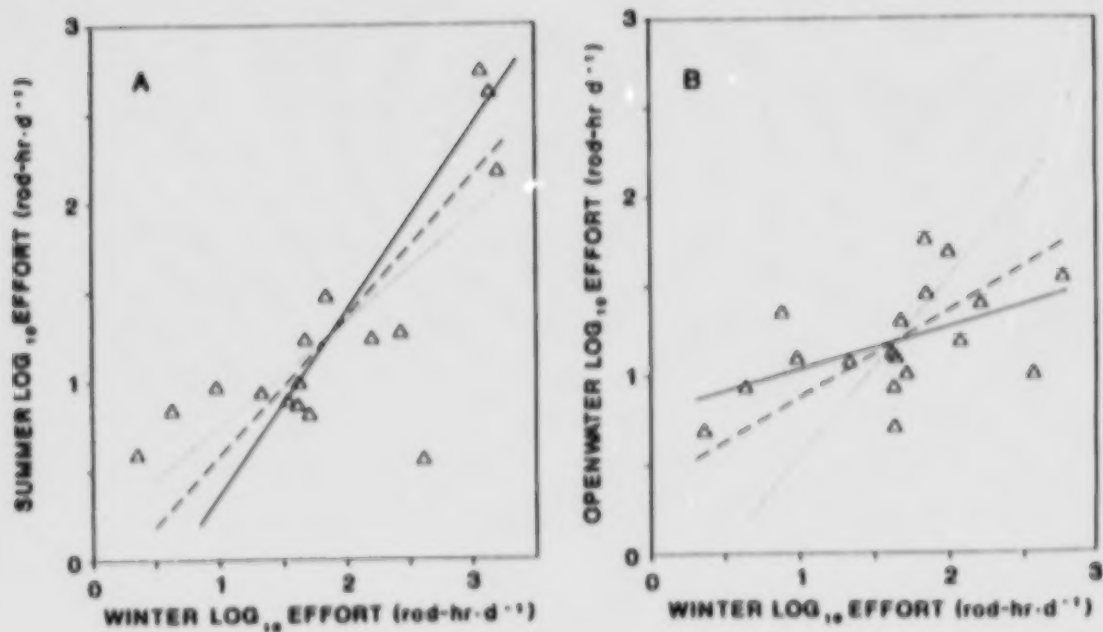


FIG. 24. Correlation of: (A) summer and winter fishing effort in rod-hours per day; and (B) open-water and winter fishing effort in rod-hours per day for lake trout in common lakes.

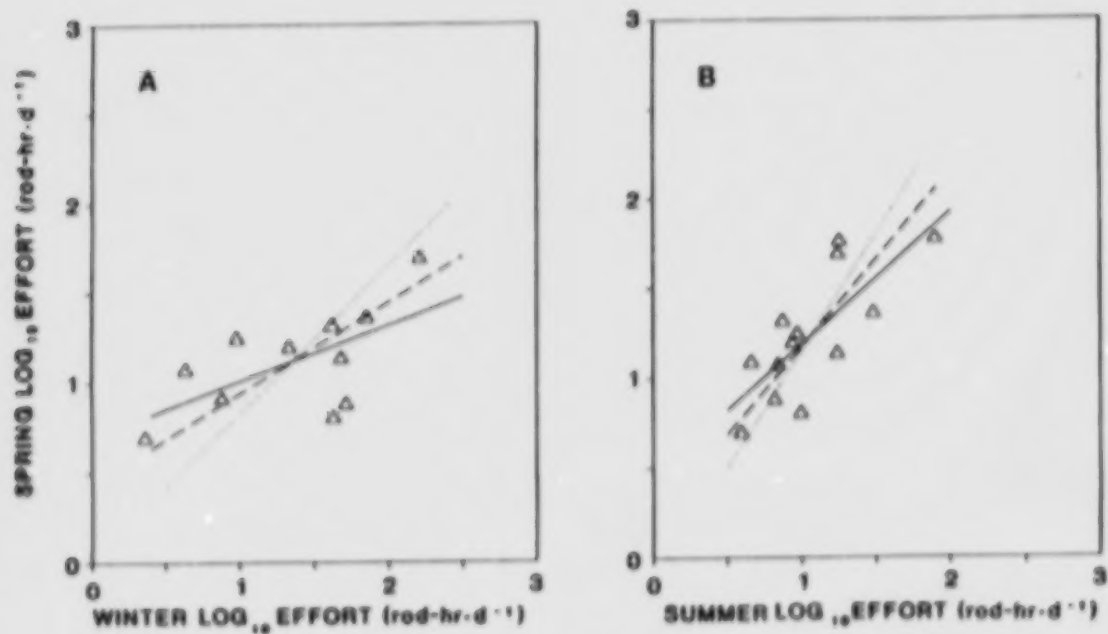


FIG. 25. Correlation of: (A) spring and winter; and (B) spring and summer fishing effort in rod-hours per day for lake trout in common lakes.

Table 17. Summary of regression analyses of interseasonal comparisons of effort and harvests of lake trout in Ontario lakes. Data pairs over seasons are from the same lake. The two predictive equations (Y on X and X on Y) and the geometric mean regression (G.M.) statistics are given for each comparison.

Seasons	Regression	# of lakes	Regression statistics				Adjusted r^2 (%)
			a	b	S_b	P	
Effort (rod-hour d^{-1}) versus effort (rod-hour d^{-1})							
Summer - winter	Y on X	16	0.151	0.593	0.137	<0.01	54
	X on Y	16	0.656	0.966	0.223	<0.01	54
	G.M.	16	-0.206	0.783			
Spring - winter	Y on X	11	0.697	0.311	0.134	0.045	31
	X on Y	11	0.005	1.205	0.518	0.045	31
	G.M.	11	0.431	0.488			
Open-water - winter	Y on X	18	0.796	0.237	0.107	0.041	19
	X on Y	18	0.456	0.995	0.448	0.041	19
	G.M.	18	0.386	0.488			
Spring - summer	Y on X	13	0.453	0.736	0.196	<0.01	52
	X on Y	13	0.114	0.766	0.203	<0.01	52
	G.M.	13	0.194	0.980			
Harvest (no. of fish d^{-1}) versus harvest (no. of fish d^{-1})							
Summer - winter	Y on X	16	-0.144	0.575	0.162	<0.01	44
	X on Y	16	0.459	0.826	0.230	<0.01	44
	G.M.	16	-0.312	0.834			
Spring - winter	Y on X	11	-0.012	0.053	0.244	ns	0
	X on Y	11	0.099	0.099	0.453	ns	0
	G.M.	11	-0.078	0.728			
Open water - winter	Y on X	13	-0.024	0.133	0.165	ns	0
	X on Y	13	0.092	0.422	0.521	ns	0
	G.M.	13	-0.199	0.561			
Spring - summer	Y on X	13	0.101	1.157	0.252	<0.01	63
	X on Y	13	-0.058	0.568	0.124	<0.01	63
	G.M.	13	0.099	1.406			

Table 17. (Continued)

Seasons	Regression	# of lakes	Regression statistics				Adjusted r^2 (%)
			a	b	S_b	P	
Harvest (kg d^{-1}) versus harvest (kg d^{-1})							
Summer - winter	Y on X	9	-0.304	0.358	0.423	ns	0
	X on Y	9	0.129	0.260	0.306	ns	0
	G.M.	9	-0.350	1.175			
Spring - winter	Y on X	10	-0.104	0.326	0.522	ns	0
	X on Y	10	0.069	0.143	0.228	ns	0
	G.M.	10	-0.479	1.513			
Open water - winter	Y on X	15	-0.064	0.437	0.174	0.026	28
	X on Y	15	0.307	0.748	0.298	0.026	28
	G.M.	15	-0.190	0.764			
Spring - summer	Y on X	12	0.099	0.771	0.242	<0.01	45
	X on Y	12	-0.177	0.653	0.205	<0.01	45
	G.M.	12	0.169	1.086			

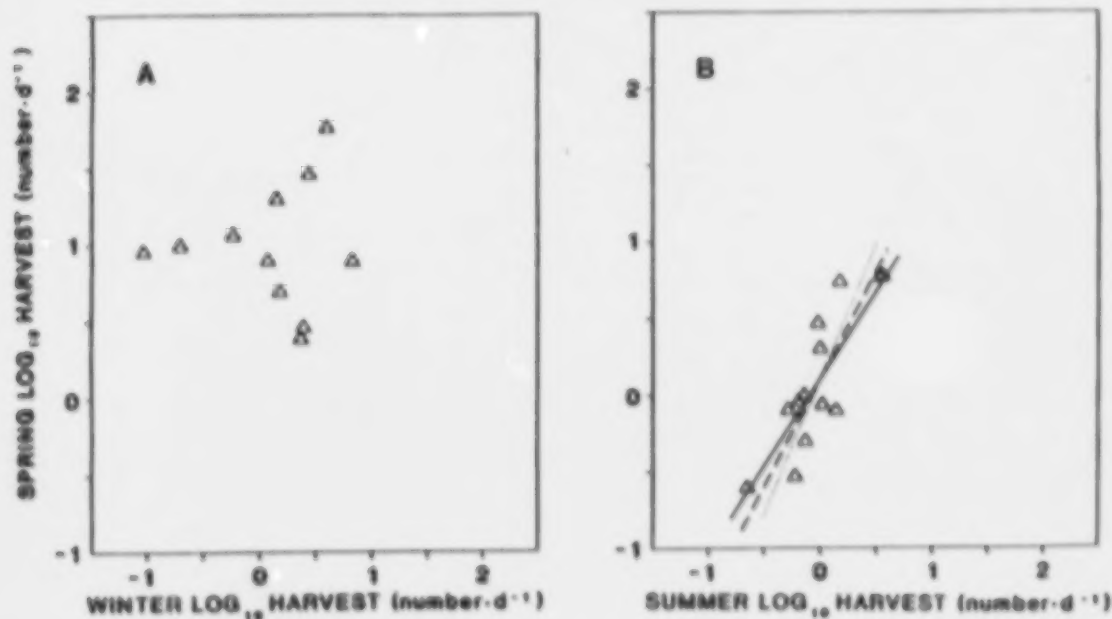


FIG. 26. Correlation of: (A) spring and winter; and (B) spring and summer harvests of lake trout in number of fish per day for sets of common lakes.

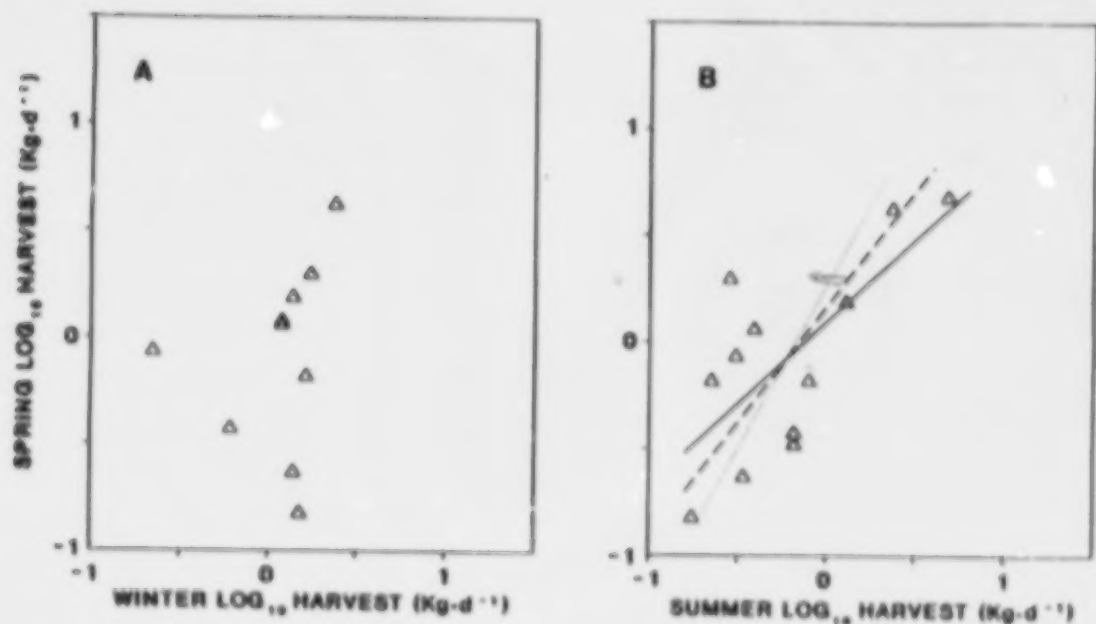


FIG. 27. Correlation of: (A) spring and winter; and (B) spring and summer harvest of lake trout in weight (kg) of fish per day for sets of common lakes.

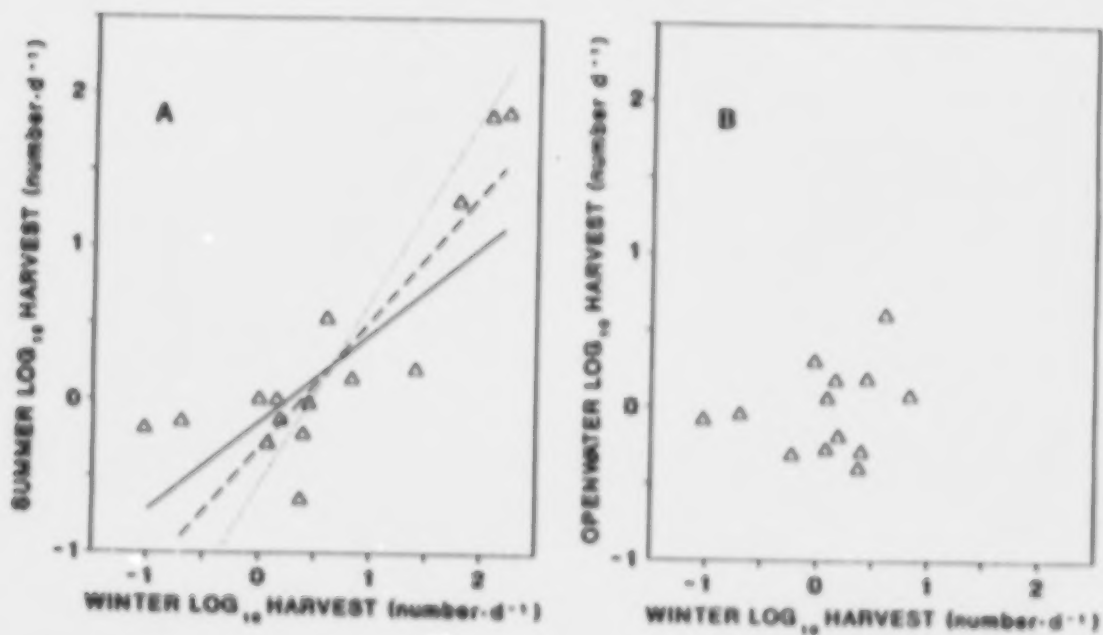


FIG. 28. Correlation of: (A) summer and winter; and (B) open-water and winter harvests of lake trout in number of fish per day for sets of common lakes.

nor summer harvest in weight (Fig. 29a) are predictable from winter harvests for existing data. Summer harvest in number of fish, however, is significantly correlated with winter harvest (Fig. 28a), and open-water harvest in weight, which is also correlated with winter harvest (Fig. 29b). These correlations might be useful as a first order approximation of fishing effort and total harvests, when actual harvests are known for only one season, although we caution that major variation exists.

Harvests and Yields of Native Versus Stocked Lake Trout Populations

We compared effort and harvest statistics for angling fisheries exploiting native, unstocked lake trout populations versus those exploiting stocked populations. We have addressed two specific null hypotheses: stocked and unstocked lakes receive similar fishing pressure; and stocked and unstocked lakes produce similar harvests of lake trout. These hypotheses were assessed using four approaches: (1) simple description of fishing intensity, yield, and HUE means for N1 and N3 status populations (Table 1) among seasons and regions; (2) ANCOVA to compare effort versus area; and harvest and yield versus effort and area relationships for unstocked lakes and two categories of stocked lakes, lakes that had been stocked for 1-3 yr and those that had been stocked for >3 yr (the analyses were run for winter and open-water fisheries); (3) ANCOVA comparing harvest and yield for status N1

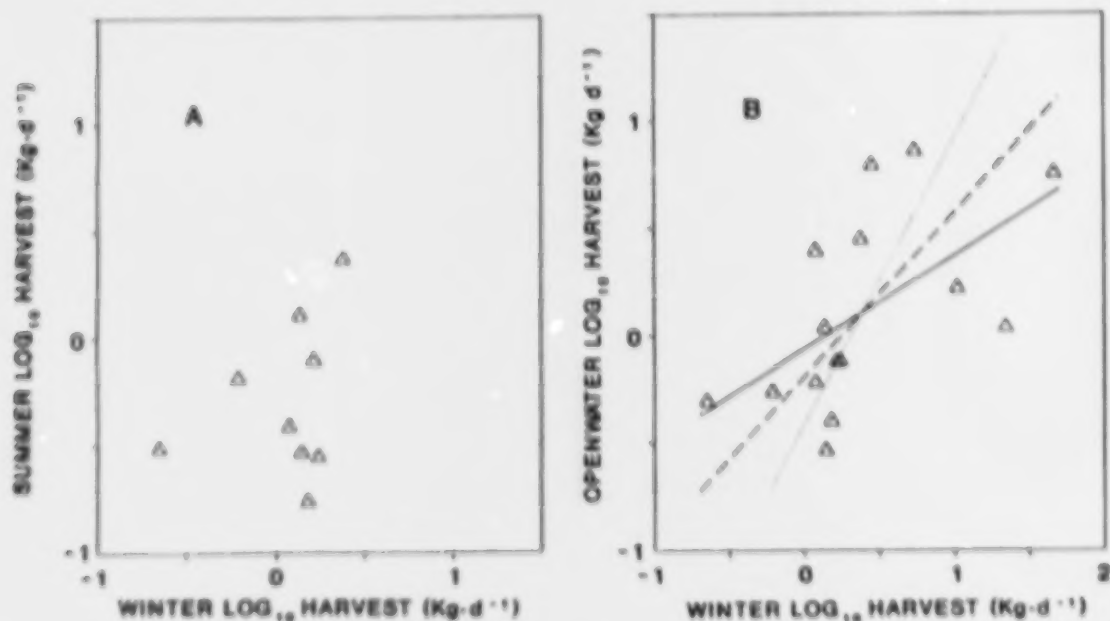


FIG. 29. Correlation of: (A) summer and winter; and (B) open-water and winter harvests of lake trout in weight of fish per day for sets of common lakes.

stocks versus status N3 stocks; and (4) chi-square analysis of annual yield versus fishing intensity for N1 versus N3 - status populations.

Fishing efforts, harvests and yields for N1 and N3 stocks - Fishing intensity, yield, HUE, and mean body weight of harvested fish for unstocked, self-sustaining wild populations of lake trout (status N1, Table 1) and stocked partly self-sustained populations (status N3, Table 1) are summarized by season in Tables 18a and 18b. In each season of the year, fishing intensity was greater on stocked lakes. During winter, average (geometric mean) yield in number and weight was decidedly higher for stocked populations than for wild populations (1.32 versus 0.17 fish ha⁻¹ and 0.30 versus 0.17 kg ha⁻¹, respectively). Annual yields in number and weight were greater for wild than for stocked populations (0.91 versus 0.71 fish ha⁻¹ and 0.62 and 0.50 kg ha⁻¹, respectively). Spring yields followed a similar pattern of greater production in unstocked lakes, but summer yields were higher for stocked populations. The effort during summer, however, was three times higher in stocked than unstocked lakes (Table 18a). In all seasons, average HUE was higher for wild than for stocked populations (Table 18b). These patterns generally persisted when the same data were further partitioned within season into northern and southern Ontario populations (Tables 19a, b). Yields were higher in the north than the south, except for winter fisheries, which were mainly based on stocked populations in the south. In general, fishing intensity was much higher on stocked lakes than unstocked lakes, but yields were actually higher or similar in unstocked lakes except during winter. HUE was usually lower in stocked lakes, suggesting lower quality of fishing in stocked lakes (Table 19b). These comparisons must be interpreted cautiously, however, because of the small sample sizes and large amount of variation among lakes.

Comparison of lakes stocked for 1-3 yr and >3 yr - The effort and harvest statistics for stocked and unstocked lakes are summarized in Table 20. Effort-area relationships and least-square means did not differ between stocked and unstocked lakes during either winter or open-water seasons (Fig. 30) (ANCOVA for adjusted means: Type III SS, $F = 0.15$, $P = 0.87$; $F = 1.09$, $P = 0.35$). For the winter fisheries, a near significant stocking effect on harvest in number was revealed by ANCOVA (Type III SS, $F = 3.30$, $P = 0.056$) when effort and area were run as covariates (Fig. 31), however, the effect was not significant for harvest expressed in weight ($F = 2.40$, $P = 0.11$). The winter mean HUE in number of fish for the three categories of lakes, calculated from Table 20, are; unstocked 0.075, stocked 1-3 yr 0.133, and stocked >3 yr 0.116 fish hr⁻¹ after adjustment to the overall winter

TABLE 18a. Comparison of fishing intensity and yield in number and weight of lake trout in various seasons of the year for wild, unstocked (N1), and stocked (N3) lake trout populations in inland lakes in Ontario. Duration for the annual data is the entire open-fishing season which, in some cases, excludes the winter season.

Season (observed duration)	Status of stock	Fishing intensity				Yield				Yield			
		$\log_{10} \text{ h ha}^{-1} \text{ d}^{-1}$			h ha^{-1} season ⁻¹	$\log_{10} \text{ no ha}^{-1} \text{ d}^{-1}$			no ha^{-1} season ⁻¹	$\log_{10} \text{ kg ha}^{-1} \text{ d}^{-1}$			kg ha^{-1} season ⁻¹
		n	mean	sd		n	mean	sd		n	mean	sd	
Winter (86 d)	N1	12	-1.59	0.48	2.34	9	-2.74	0.47	0.17	10	-2.74	0.55	0.17
	N3	27	-0.93	0.61	10.69	16	-1.84	0.73	1.32	22	-2.48	0.51	0.30
	Total	47	-1.17	0.64	6.15	31	-2.19	0.74	0.59	37	-2.56	0.56	0.25
Spring (46 d)	N1	14	-1.39	0.37	2.49	14	-2.30	0.53	0.31	7	-2.48	0.61	0.20
	N3	8	-1.24	0.34	3.51	8	-2.44	0.65	0.22	8	-2.58	0.65	0.16
	Total	25	-1.34	0.34	2.79	25	-2.35	0.54	0.27	18	-2.49	0.56	0.20
Summer (106 d)	N1	6	-1.79	0.62	1.49	6	-2.74	0.78	0.17	4	-3.29	0.93	0.05
	N3	12	-1.30	0.37	4.61	12	-2.36	0.57	0.40	7	-2.82	0.51	0.14
	Total	21	-1.45	0.47	3.26	21	-2.49	0.61	0.30	14	-2.89	0.64	0.12
Open-water (151 d)	N1	17	-1.65	0.37	3.43	14	-2.52	0.42	0.46	9	-2.77	0.32	0.26
	N3	22	-1.54	0.52	4.41	8	-2.63	0.46	0.36	20	-2.74	0.51	0.28
	Total	47	-1.57	0.49	4.12	26	-2.59	0.46	0.39	37	-2.71	0.53	0.30
Annual	N1	24	0.79	0.40	6.17	24	-0.04	0.46	0.91	20	-0.21	0.38	0.62
	N3	17	0.93	0.35	8.51	17	-0.15	0.38	0.71	16	-0.30	0.30	0.50
	Total	49	0.90	0.38	7.94	49	-0.06	0.42	0.87	43	-0.20	0.37	0.63

Table 18b. Comparison of harvest-per-unit-effort (HUE) in number and weight of lake trout in various seasons of the year for wild, unstocked (N1), and stocked (N3) lake trout populations in inland Ontario lakes. Duration for the annual data is the entire open-fishing season which, in some cases, excludes the winter season. Durations for the other seasons are the actual number of observed days of fishing (Table 15).

Season (observed duration)	Status of stock	HUE ¹			Actual HUE no. fish	HUE ²			Actual HUE wt. (kg)	n	Mean body weight (kg)
		log ₁₀ no. of fish				log ₁₀ wt. of fish (kg)					
		n	mean	sd		n	mean	sd			
Winter (86 d)	N1	18	-0.92	0.34	0.12	15	-1.06	0.25	0.09	15	0.72
	N3	30	-1.09	0.30	0.08	31	-1.39	0.28	0.04	30	0.50
	Total	60	-1.02	0.31	0.10	56	-1.23	0.32	0.06	56	0.62
Spring (46 d)	N1	14	-0.88	0.27	0.13	7	-0.98	0.41	0.11	7	0.79
	N3	9	-1.14	0.32	0.07	4	-1.33	0.25	0.05	4	0.65
	Total	26	-0.99	0.30	0.10	11	-1.08	0.36	0.08	11	0.81
Summer (106 d)	N1	6	-0.98	0.29	0.11	5	-1.20	0.44	0.06	5	0.60
	N3	14	-1.01	0.26	0.10	5	-1.31	0.16	0.05	5	0.50
	Total	24	-1.05	0.30	0.09	12	-1.23	0.32	0.06	12	0.66
Open-water (151 d)	N1	20	-0.89	0.24	0.13	14	-1.11	0.39	0.08	14	0.60
	N3	14	-1.05	0.31	0.09	20	-1.22	0.33	0.06	14	0.68
	Total	42	-1.02	0.33	0.10	45	-1.15	0.34	0.07	42	0.74
Annual	N1	24	-0.84	0.23	0.15	20	-0.98	0.25	0.11	20	0.72
	N3	17	-1.08	0.22	0.08	16	-1.27	0.18	0.05	16	0.65
	Total	49	-0.96	0.26	0.11	43	-1.10	0.26	0.08	43	0.72

TABLE 19a. Comparison of fishing intensity and yield in number and weight of lake trout in northern and southern Ontario, and various seasons of the year for wild, unstocked (N1) and stocked (N3) lake trout populations in inland lakes. Duration of the annual data is the entire open-fishing season which, in some cases, excludes the winter season.

Season (observed duration)	Region of Ontario	Status of stock	Fishing intensity				Yield				Yield			
			$\log_{10} \text{ h ha}^{-1} \text{ d}^{-1}$			h ha^{-1} season ⁻¹	$\log_{10} \text{ no. ha}^{-1} \text{ d}^{-1}$			no. ha^{-1} season ⁻¹	$\log_{10} \text{ kg ha}^{-1} \text{ d}^{-1}$			kg ha^{-1} season ⁻¹
			n	mean	sd		n	mean	sd		n	mean	sd	
Winter (90 d)	North	N1	4	-1.87	0.37	1.23	4	-2.86	0.24	0.13	3	-3.18	0.32	0.06
		N3	0	.	.	.	0	.	.	.	0	.	.	.
		Total	5	-1.85	0.32	1.29	5	-2.79	0.26	0.15	4	-3.15	0.27	0.06
	South	N1	8	-1.45	0.49	3.23	5	-2.64	0.61	0.21	7	-2.55	0.53	0.26
		N3	27	-0.93	0.61	10.69	16	-1.84	0.73	1.32	22	-2.48	0.51	0.30
		Total	42	-1.09	0.62	7.40	26	-2.08	0.75	0.76	33	-2.48	0.55	0.30
Spring (61 d)	North	N1	3	-1.29	0.36	3.13	3	-2.05	0.38	0.54	1	-2.43	.	0.23
		N3	0	.	.	.	0	.	.	.	0	.	.	.
		Total	3	-1.29	0.36	3.13	3	-2.05	0.38	0.54	1	-2.43	.	0.23
	South	N1	11	-1.42	0.38	2.32	11	-2.36	0.56	0.27	6	-2.48	0.67	0.20
		N3	8	-1.24	0.34	3.51	8	-2.44	0.65	0.22	8	-2.58	0.65	0.16
		Total	22	-1.34	0.34	2.79	22	-2.39	0.55	0.25	17	-2.50	0.58	0.19
Summer (106 d)	North	N1	0	.	.	.	0	.	.	.	0	.	.	.
		N3	1	-1.23	.	5.42	1	-2.32	.	0.44	1	-2.43	.	0.34
		Total	1	-1.23	.	5.42	1	-2.32	.	0.44	1	-2.43	.	0.34
	South	N1	6	-1.79	0.62	1.49	6	-2.74	0.78	0.17	4	-3.29	0.93	0.05
		N3	11	-1.30	0.38	4.61	11	-2.36	0.59	0.40	6	-2.88	0.53	0.12
		Total	20	-1.46	0.48	3.19	20	-2.50	0.62	0.29	13	-2.92	0.65	0.11
Open-water (151 d)	North	N1	6	-1.42	0.26	5.82	6	-2.32	0.36	0.73	2	-2.52	0.11	0.42
		N3	1	-1.40	.	6.09	1	-2.66	.	0.33	1	-2.79	.	0.25
		Total	18	-1.43	0.22	5.68	8	-2.37	0.33	0.65	4	-2.50	0.26	0.48
	South	N1	11	-1.78	0.36	2.54	8	-2.67	0.41	0.33	7	-2.85	0.33	0.22
		N3	21	-1.55	0.53	4.31	7	-2.63	0.49	0.36	19	-2.74	0.52	0.28
		Total	39	-1.60	0.53	3.84	18	-2.69	0.48	0.31	33	-2.73	0.55	0.28
Annual	North	N1	15	0.87	0.36	7.41	15	0.04	0.48	1.10	12	-0.18	0.41	0.66
		N3	9	1.00	0.25	10.00	9	-0.11	0.31	0.78	9	-0.27	0.30	0.54
		Total	29	0.98	0.35	9.55	29	0.01	0.43	1.02	26	-0.16	0.39	0.69
	South	N1	9	0.66	0.43	4.57	9	-0.17	0.43	0.68	8	-0.26	0.35	0.55
		N3	8	0.85	0.45	7.08	8	-0.20	0.47	0.63	7	-0.33	0.33	0.47
		Total	20	0.78	0.41	6.03	20	-0.17	0.40	0.68	17	-0.27	0.32	0.54

TABLE 19b. Comparison of harvest-per-unit-effort (HUE) in number and weight of lake trout in northern and southern Ontario and various seasons of the year for wild, unstocked (N1), and stocked (N3) lake trout populations in inland lakes. Duration of the annual data is the entire open-fishing season which, in some cases, excludes the winter season.

Season (observed duration)	Region of Ontario	Status of stock	HUE ¹			Actual HUE no. fish	HUE ¹			Actual HUE no. fish	n	Mean body weight (kg)
			log ₁₀ no. of fish				log ₁₀ wt. of fish (kg)					
			n	mean	sd		n	mean	sd			
Winter (90 d)	North	N1	13	-0.96	0.35	0.11	9	-1.05	0.28	0.09	9	0.81
		N3	9	-0.88	0.15	0.13	9	-1.38	0.27	0.04	9	0.32
		Total	28	-0.92	0.27	0.12	24	-1.13	0.32	0.07	24	0.62
	South	N1	5	-0.80	0.30	0.16	6	-1.08	0.22	0.08	5	0.53
		N3	21	-1.18	0.30	0.07	22	-1.39	0.30	0.04	21	0.62
		Total	32	-1.10	0.32	0.08	32	-1.30	0.30	0.05	32	0.63
Spring (61 d)	North	N1	4	-0.77	0.03	0.17	1	-0.74	.	0.18	1	1.07
		N3	0	.	.	.	0	.	.	.	0	.
		Total	4	-0.77	0.03	0.17	1	-0.74	.	0.18	1	1.07
	South	N1	10	-0.93	0.32	0.12	6	-1.02	0.43	0.10	6	0.81
		N3	9	-1.14	0.32	0.07	4	-1.33	0.25	0.05	4	0.65
		Total	22	-1.03	0.32	0.09	12	-1.11	0.36	0.08	12	0.83
Summer (106 d)	North	N1	1	-1.21	.	0.06	0	.	.	.	0	.
		N3	1	-1.10	.	0.08	1	-1.22	.	0.06	1	0.76
		Total	2	-1.16	0.08	0.07	1	-1.22	.	0.06	1	0.87
	South	N1	5	-0.93	0.30	0.12	5	-1.20	0.44	0.06	5	0.54
		N3	13	-1.00	0.27	0.10	4	-1.33	0.17	0.05	4	0.47
		Total	22	-1.04	0.31	0.09	11	-1.23	0.33	0.06	11	0.65
Open-water (151 d)	North	N1	12	-0.94	0.23	0.11	7	-1.05	0.51	0.09	7	0.78
		N3	6	-1.09	0.25	0.08	1	-0.74	.	0.18	1	2.24
		Total	23	-1.05	0.27	0.09	13	-1.07	0.44	0.09	13	0.95
	South	N1	8	-0.82	0.24	0.15	7	-1.17	0.26	0.07	7	0.45
		N3	8	-1.02	0.36	0.10	19	-1.24	0.32	0.06	8	0.60
		Total	19	-0.99	0.39	0.10	32	-1.18	0.29	0.07	19	0.65
Annual	North	N1	15	-0.84	0.22	0.14	12	-1.04	0.20	0.09	12	0.63
		N3	9	-1.11	0.27	0.08	9	-1.22	0.20	0.06	9	0.78
		Total	29	-0.98	0.27	0.11	26	-1.11	0.23	0.08	26	0.74
	South	N1	9	-0.83	0.27	0.15	8	-0.88	0.30	0.13	8	1.07
		N3	8	-1.05	0.17	0.09	7	-1.33	0.15	0.05	7	0.53
		Total	20	-0.95	0.24	0.11	17	-1.09	0.31	0.08	17	0.72

TABLE 20. Summary of fishing effort (angler-hours) and harvest of lake trout in unstocked lakes and two categories of stocked lakes, those stocked 1-3 yr, and those stocked >3 yr from 1980-1986. Analyses are for fisheries during winter, open-water, and winter and open-water combined. The observed harvests and yields are reported at the corresponding mean levels of effort and fishing intensity for each stocking category. The adjusted means are calculated at the mean level of effort over all stocking categories within each season for surveys reported in either number or kg of fish.

Stocking status	Mean area (ha)	Effort		Number of fish				Effort		Kilograms of fish			
		d ¹	ha ⁻¹ d ¹	(d ¹)		(ha ⁻¹ d ¹)		d ¹	ha ⁻¹ d ¹	(d ¹)		(ha ⁻¹ d ¹)	
		(h)	(h)	obs.	adj.	obs.	adj.	(h)	(h)	obs.	adj.	obs.	adj.
<u>Winter</u>													
Natural no. lakes	1820 10	30.21 7	0.02 7	2.33 7	2.75 7	0.0018 7	0.0051 7	72.91 9	0.03 9	8.55 9	5.01 9	0.0030 9	0.0046 9
Stocked 1-3 yr no. lakes	437 23	25.93 14	0.05 14	2.38 14	4.89 14	0.0046 14	0.0065 14	49.52 18	0.08 18	2.51 18	2.52 18	0.0040 18	0.0028 18
Stocked >3 yr no. lakes	1380 14	80.07 10	0.02 10	7.11 10	4.26 10	0.0100 10	0.0080 10	44.69 10	0.03 10	2.36 10	2.37 10	0.0017 10	0.0027 10
<u>Open-water</u>													
Natural no. lakes	1202 17	35.39 14	0.03 14	3.48 14	2.15 14	0.0034 14	0.0025 14	35.02 10	0.02 10	2.90 10	1.72 10	0.0016 10	0.0021 10
Stocked 1-3 yr no. lakes	501 19	10.12 5	0.02 5	0.86 5	1.09 5	0.0020 5	0.0022 5	21.69 17	0.03 17	1.36 17	1.01 17	0.0022 17	0.0018 17
Stocked >3 yr no. lakes	1660 11	20.50 7	0.03 7	1.95 7	1.88 7	0.0031 7	0.0027 7	22.81 10	0.01 10	1.89 10	2.06 10	0.0009 10	0.0022 10
<u>Winter and Open-water</u>													
Natural no. lakes	1413 27	33.69 21	0.03 21	3.06 21	3.29 21	0.0028 21	0.0045 21	49.45 19	0.03 19	4.33 19	2.84 19	0.0013 19	0.0024 19
Stocked 1-3 yr no. lakes	468 42	19.51 19	0.04 19	1.75 19	3.44 19	0.0036 19	0.0042 19	33.57 35	0.05 35	1.88 35	2.02 35	0.0022 35	0.0032 35
Stocked >3 yr no. lakes	1479 25	50.00 17	0.07 17	4.54 17	3.15 17	0.0066 17	0.0042 17	33.08 20	0.02 20	2.13 20	2.05 20	0.0030 20	0.0023 20

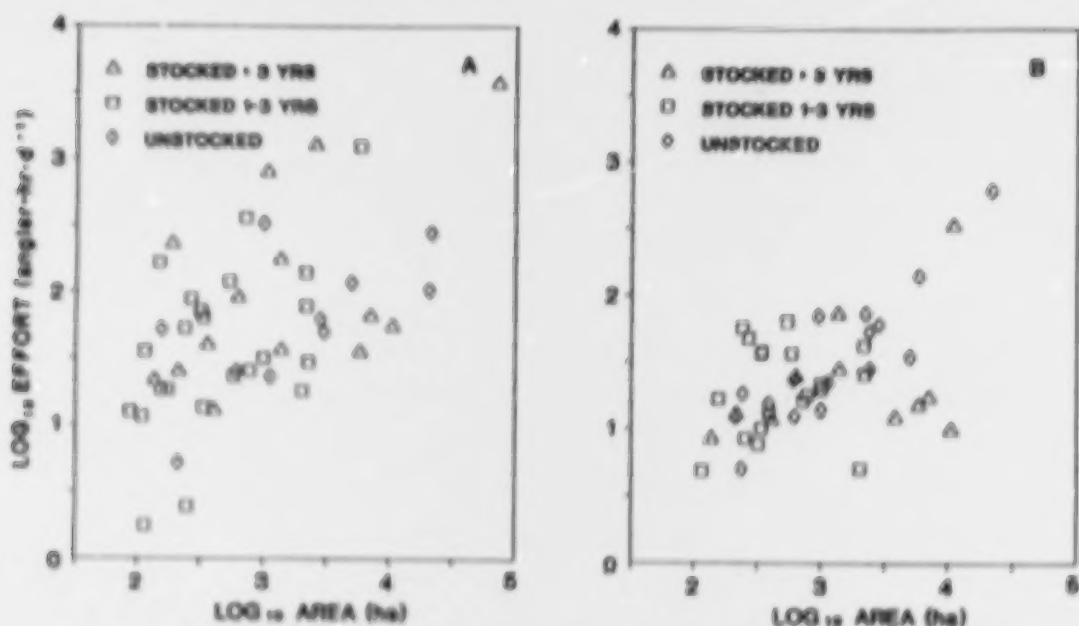


FIG. 30. Correlation between fishing effort in angler-hours per day during winter (A) and open-water (B) fishing seasons and lake area for stocked and unstocked lake trout lakes in Ontario. Only stocking occurring after 1980 was considered.

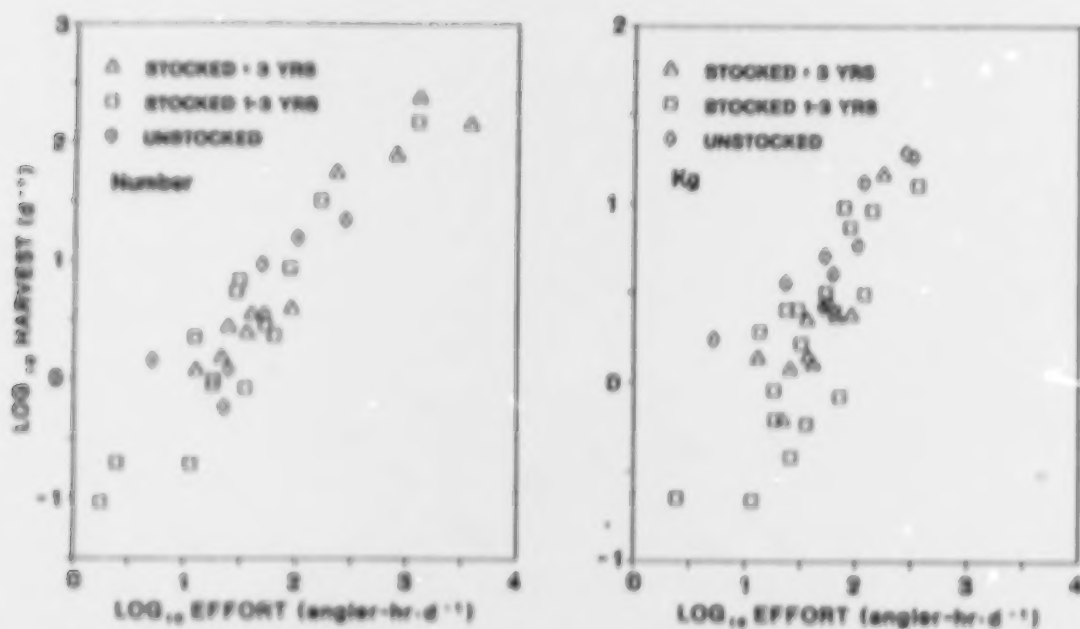


FIG. 31. Correlation between harvest of lake trout per day in number and weight of fish and fishing effort in angler-hours per day during the winter fishing season for stocked and unstocked lake trout lakes in Ontario. Only stocking occurring after 1980 was considered.

effort of 36.77 hr d^{-1} . Similarly, for harvest in weight, the adjusted winter harvests are; unstocked 0.095, stocked 1-3 yr 0.048, stocked >3 yr 0.045 kg hr^{-1} (Table 20). Thus, the number of fish harvested is greater in stocked lakes, but the biomass of fish harvested is greater in unstocked lakes as is the body weight of individual fish. The slope of the relationships between harvest and effort did not differ for stocked versus unstocked populations.

For winter fisheries, significant differences were not found between lakes of different stocking status, when yield was expressed in number or weight of fish versus fishing intensity (Fig. 32), yield in number being: unstocked 0.0027, stocked 1-3 yr 0.0038, and stocked >3 yr 0.0044 $\text{fish ha}^{-1}\text{d}^{-1}$ at a common effort of 0.05 angler $\text{h ha}^{-1}\text{d}^{-1}$ and yield in kg being: unstocked 0.0044, stocked 1-3 yr 0.0027, stocked >3 yr 0.0026 $\text{kg ha}^{-1}\text{d}^{-1}$ also at a common effort of 0.05 angler $\text{h ha}^{-1}\text{d}^{-1}$ (Table 20). These values can be converted to season estimates by multiplying by winter duration (90 d).

Similarly, ANCOVA (Type III SS) did not reveal a significant effect of stocking status for open-water fisheries for the particular lakes and circumstances represented in our data set, whether expressed as total harvest (Fig. 33) or yield (Fig. 34).

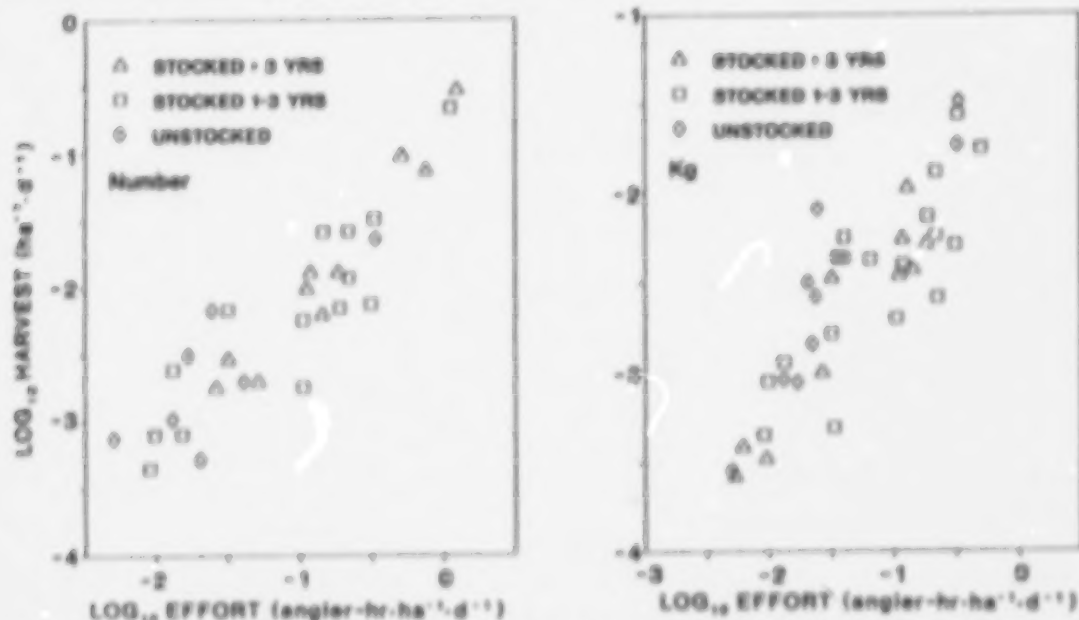


FIG. 32. Correlation between yield of lake trout per ha per day in number and weight (kg) of fish and fishing effort in angler-hours per ha per day during the winter fishing season for stocked and unstocked lake trout lakes in Ontario. Only stocking occurring after 1980 was considered.

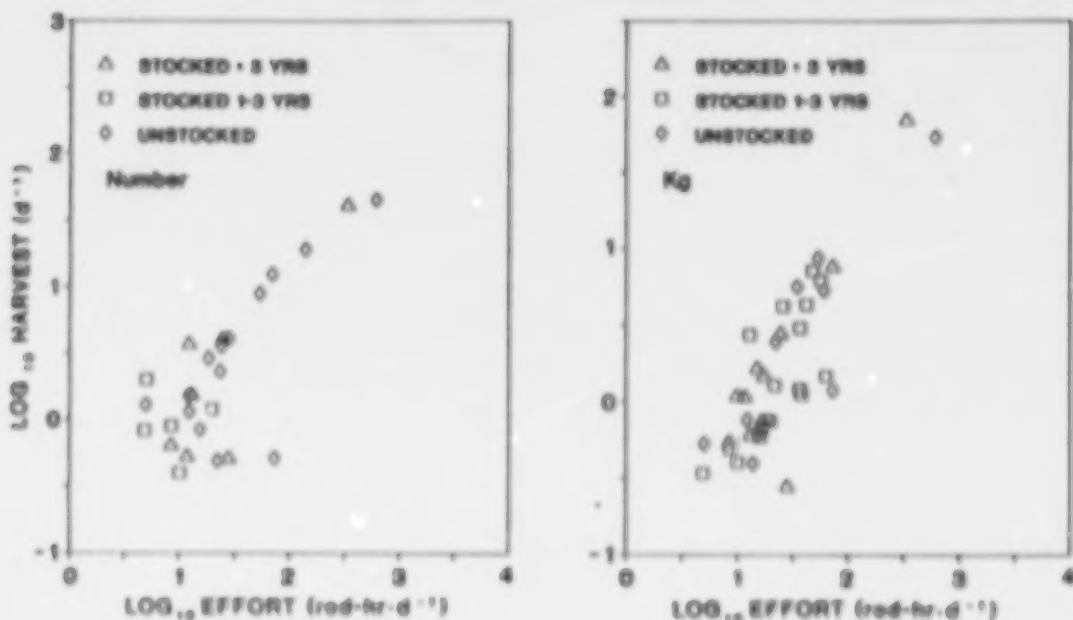


FIG. 33. Correlation between harvest of lake trout per day in number and weight of fish and fishing effort in rod-hours per day during the open-water fishing season for stocked and unstocked lake trout lakes in Ontario. Only stocking occurring after 1980 was considered.

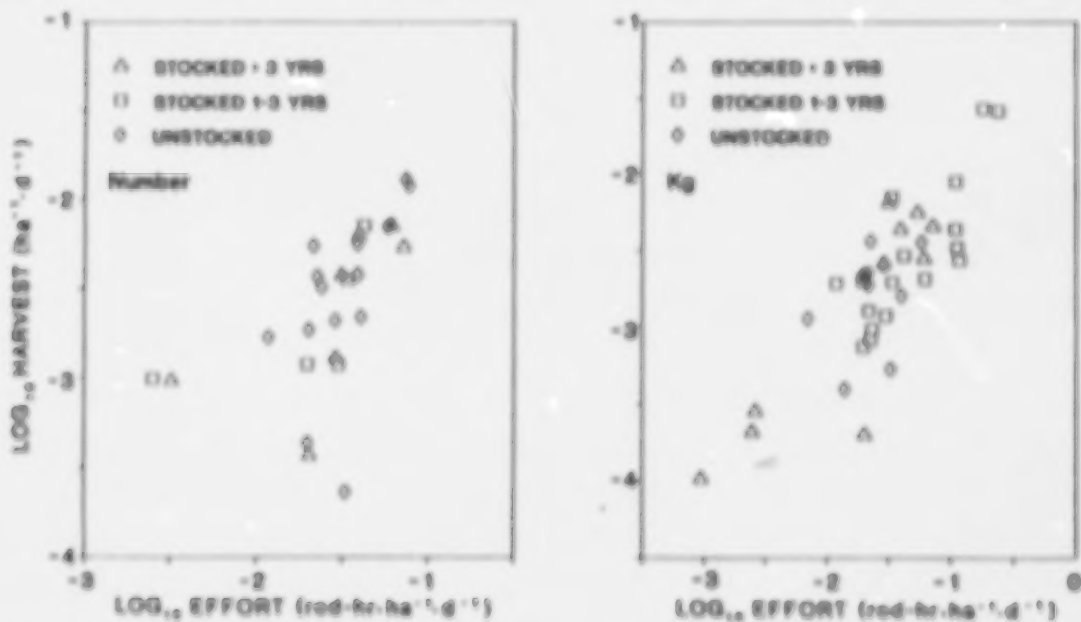


FIG. 34. Correlation between yield of lake trout per ha per day in number and weight (kg) of fish and fishing effort in rod-hours per ha per day during the open-water fishing season for stocked and unstocked lake trout lakes in Ontario. Only stocking occurring after 1980 was considered.

Although not statistically significant, yield in number of fish for winter fisheries was 20-40% higher in stocked lakes but, in contrast, yield in weight in the same lakes was only about 60% of the yield for unstocked wild populations. The harvests and yields for open-water fisheries are similar for unstocked, self-sustaining versus stocked populations (Table 20).

Comparison of harvests of N1 and N3 populations - ANCOVA, using a group slope analysis with fishing effort, TDS, secchi depth, mean depth, and NHV as covariates, revealed no significant differences in harvest in number or weight between fisheries on N1 and N3 populations during either winter or open-water seasons. For winter fisheries, however, the adjusted or least square mean harvests for N1 versus N3 populations were: N1 = 2.64, N3 = 5.47 fish d^{-1} ($F = 2.21$, $P = 0.16$); and N1 = 3.45, N3 = 2.13 kg d^{-1} ($F = 3.43$, $P = 0.08$). Similar analyses for annual harvests revealed that fisheries on N1 populations had higher harvests in both number and kg of fish with adjusted means as follows: N1 = 446, N3 = 215 fish yr^{-1} ($F = 8.74$, $P = 0.007$); and N1 = 232, N3 = 136 kg yr^{-1} ($F = 7.58$, $P = 0.012$).

Chi-square analysis of annual yield of N1 versus N3 populations - The yields and fishing intensities for annual fisheries of N1 and N3 status populations shown in Fig. 13 were compared in 2×2 chi-square analyses for both number and weight of fish harvested. The number of populations within each status category above or below the least-square regression line were compared to the null hypothesis expectation where harvests of both types of populations are the same. Yields of wild, self-sustaining populations, both in number and weight of fish taken, were more frequently above the common regression for these populations, as indicated by chi-square values of 8.92 ($P < 0.01$) and 9.04 ($P < 0.01$), respectively. N1 (wild) populations, therefore, had higher yields than N3 (stocked) populations after correction for area and effort effects.

Summary of stocking effects - In general, harvests and yields of wild, naturally self-sustaining lake trout populations were as high or higher than those populations receiving supplemental stocking. The major exception to this was for yield in numbers of fish for winter fisheries. In that case, more fish were harvested from stocked lakes, but they weighed less on average (Table 18b) and the weight of fish harvested ha^{-1} was less than for unstocked lakes. This suggests that stocked lakes have been overharvested, especially during winter, and that stocking is simply supplying harvests of small immature fish in excess of the self-sustaining capacity of the natural lake trout production systems.

While the relationship between fishing effort and area did not differ between stocked and unstocked lakes, the mean fishing intensity on stocked lakes was 4.6, 1.4, and 3.1 times higher than on unstocked lakes during winter, spring, and summer, respectively. Stocking, therefore, is effective in maintaining fishing effort at a high level (on N3 status lakes), even though HUE on stocked lakes is only about 50% of winter levels and 75% of summer levels of N1 status lakes (Table 18b). Stocking also enables more small fish to be harvested than otherwise possible at comparable high fishing rates, because stocking can provide juvenile fish at a higher rate than is possible through natural reproduction. If those fish are harvested at a younger age and smaller body size, more fish will potentially be available, but if the mean age of harvest is below the age at which biomass is maximized, yield in kg will decline (as appears to be the case for winter fisheries on stocked populations). Population biomass increases with mean age up to a maximum only while production, due to recruitment and growth of individuals, exceeds the loss of biomass due to mortality. Reduced harvest rates, therefore, could result in higher biomass yields, even without stocking, provided that other stressors or habitat factors are not limiting recruitment. Gains in numbers of fish harvested that are achieved by stocking are minimal, assuming that the natural production system has not been damaged through loss of habitat or other environmental degradation.

If stocking stimulates or maintains exploitation rates at very high levels, as appears to be the case, fisheries will become completely dependent on artificial recruitment, because few fish will escape to reach maturity. Initially, stocking will tend to mask the effects of overexploitation, but eventually, all wild fish will be lost and the proximate causes will be recognized only too late to reverse the changes. The population dynamics and implications for change in genetic composition of heavily exploited, stocked populations is addressed later in this report (p. 123, 127).

EUTROPHICATION, NURSERY HABITAT, AND PRODUCTION OF LAKE TROUT LAKES

Increased nutrient loading of oligotrophic lakes from any of several anthropogenic sources can eventually affect both the quality and the quantity of suitable lake trout habitat. The general effects of this type of eutrophication on lake trout have been examined by Ryder and Johnson (1972) and are reviewed by Evans et al. (1991) in the context of domestic and industrial effluents. The relation between nutrient loading, chlorophyll concentration, and hypolimnetic oxygen depletion has been studied in detail (Cornett and Rigler 1979; Charlton 1980; Cornett 1989) and is well understood.

Any factor that effects nutrient loading will accelerate oxygen depletion rates and reduce the amount of habitat available to lake trout in oligotrophic systems. Oxygen reduction is usually most critical during thermal stratification in mid- to late summer. The amount of available lake trout habitat is restricted during that period by the deepening of the thermocline, which produces elevated and restricting temperatures, and gradual upward progression of oxygen reduction in the cold deeper waters. Compression of the available habitat in this way forces the lake trout closer together, increasing interaction and competition and the potential for cannibalism. Oxygen depletion and habitat restriction are greatest in mid- to late summer when gonads are developing. If oxygen is reduced to a level that suppresses feeding, gonadal development and gamete production could possibly be detrimentally affected, reducing reproductive potential and recruitment. Even if oxygen and temperature were reduced only slightly from preferred or optimal conditions, feeding and somatic growth would be restricted.

Since increases in nutrient loading and eutrophication would probably be gradual, changes in quality and quantity of lake trout habitat would also be very gradual. It is assumed that decreases in somatic and gonadal production would occur only in extreme conditions and that reduction in quality and quantity of habitat would initially only restrict and confound lake trout distribution and activity. If we assume that all free-swimming life stages of lake trout have approximately the same temperature and oxygen requirements, then the restriction would cause increased interaction among individuals and probably increased cannibalism, since larger individuals are strongly piscivorous. In this situation, recruitment would decline, which would lead directly to a reduction in the size of the population. Indeed, if recruitment declined because of intraspecific size-selective predation mortality, the population would eventually have fewer, small (hence younger) individuals and become senescent (Evans et al. 1991).

Although the importance of restrictive summer oxygen and temperature conditions has been considered frequently (Martin and Olver 1976; Marcus et al. 1984; Anonymous 1987; Wilson 1988), the exact effects and mechanisms have not been adequately described. One hypothesis that we examined is that restrictive environmental conditions can create increased interaction, resulting in direct intraspecific predation in lake trout populations. When the summer distribution of small (young) lake trout is known, this hypothesis provides an even more plausible explanation of the effects of hypolimnetic oxygen depletion on intraspecific size-selective mortality. From an intensive

sampling study conducted on several lakes in the Haliburton Highlands of Ontario, it was apparent that the midsummer distribution of small, juvenile lake trout is very much deeper than that of sub-adult and adult fish. This midsummer distribution is easily illustrated by results from experimental gillnetting of South Wildcat Lake, which contains indigenous lake trout (Casselman 1987). The sampling involved gillnetting each 10 m depth stratum with a range of mesh sizes (12-127 mm stretched measure) that would catch all sizes of lake trout greater than approximately 8 cm total length (TL). At the same time, the lake was electrofished in shallow water down to a depth of 3 m, confirming that small lake trout were not in shallow water. In fact, netting showed that lake trout less than 24 cm TL were not found in water shallower than approximately 30 m (Fig. 35). Most

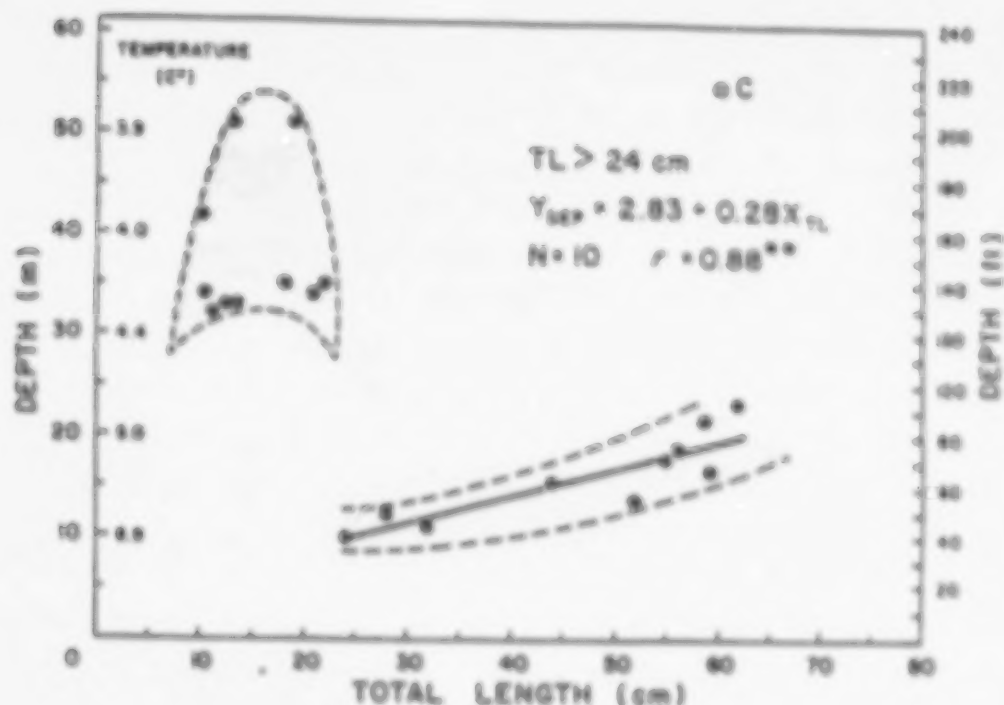


FIG. 35. The midsummer vertical distribution of lake trout in south Wildcat Lake, showing the relationship between depth and length of the lake trout. Lake trout were caught by experimental gill net ranging in mesh size from 12.5 mm to 127 mm stretched measure. Three nets were set in each of the five 10 m depth strata. Temperature and oxygen were measured during the netting study and are presented at 5 m intervals. Juvenile lake trout <24 cm total length were found in very deep water; larger fish were found in shallower water and showed a direct linear relationship with depth (as indicated on the figure). The open circle-C-indicates one very large cannibalistic lake trout found in deep water.

larger lake trout were restricted to shallower water just below the thermocline (8.4 m), and their depth distribution was directly related to size. Similar intensive sampling studies in other lakes in the Haliburton Highlands have confirmed this size-selective depth distribution of lake trout populations (J.M. Casselman, OMNR, Picton, Ont. K0K 2T0, unpubl. data).

In inland waters of Ontario, lake trout up to approximately 24 cm TL are slow growing and from 2 to 4 yrs of age; they are considered to be juveniles. Shortly after this, many individuals show a prominent increase in growth rate; these fish are considered to be subadults (approximately 5-7 yr-old). They are several years younger than adult fish, which mature, usually for the first time, at age 8. In Lake Opeongo, the FL (1941-66) of lake trout at ages 1, 2, and 3 yr was 48.6, 96.2, and 148.4 mm.

Since, as will be shown later, the optimum temperature for growth of juvenile lake trout in the laboratory is approximately the same as that selected by subadults and adults in the natural environment (10°C), the normally deep distribution of juveniles places them at a temperature much lower (approximately 4°C, ranging from 3 to 7°C; J.M. Casselman, unpubl. data) than the preferred or optimal temperature. One plausible explanation for this apparent preference for cold temperature and deep distribution is that the deep water provides a refugium which separates the small fish from the larger, potentially cannibalistic individuals, possibly resulting in greater juvenile survival. Available prey would also be less abundant in the colder waters of the hypolimnion. Preferred temperature declines at low ration (Mac 1985) and growth conversion efficiency increases as food ration declines at a given temperature (Brett et al. 1969; Brett 1971), however, which would partially offset the disadvantages of inhabiting the deep hypolimnion.

With increased human utilization, development, and resulting eutrophication, lake trout populations in some lakes have decreased, and the few fish that remain are often quite large and sometimes very old (J.M. Casselman, unpubl. data, and observations of OMNR Eastern Region districts). These senescent populations indicate that regular recruitment is not occurring and that they are probably not self-sustaining and, indeed, threatened by extinction. Fisheries managers have usually responded by stocking lakes having these types of populations with hatchery-reared lake trout.

With increased eutrophication, the quality and quantity of lake trout habitat is reduced and oxygen depletion in the hypolimnion, especially during mid- to late summer when conditions are most extreme, forces the young lake trout into shallower depths, closer to, and in the extreme, among the larger fish, making them increasingly more vulnerable to cannibalism. Two hypotheses are suggested in the above scenario: (1) lake trout recruitment is dependent upon the availability of well oxygenated water in the hypolimnion; and (2) cannibalism is a significant regulator of juvenile mortality in lake trout.

THE NURSERY-HABITAT-RECRUITMENT HYPOTHESIS

Our purpose was to investigate the hypothesis that reduced hypolimnetic oxygen causes reduced recruitment of lake trout. Specifically, we have addressed two questions: (1) whether juvenile and adult lake trout are spatially segregated during summer thermal stratification; and (2) whether different levels of natural recruitment are correlated with differences in the quality and quantity of deep-water habitat during summer.

Summer Habitat Requirements

Descriptive criteria must be developed on the spatial and temporal aspects of lake trout habitat before the quality of the habitat can be evaluated and quantified. To describe the environmental requirements and the conditions normally frequented by lake trout during summer stratification, a literature review was conducted of temperature, oxygen, and depth requirements and preferences of lake trout under natural and laboratory conditions.

The mean median depth distribution of juvenile lake trout in inland lakes in midsummer was calculated from observational data published by Dymond et al. (1929), Greeley (1929), Royce (1951), Martin (1952), Rawson and Atton (1953), Eachmeyer (1956, 1957), De Roche (1969), and Johnson (1975). Similar types of depth distribution data were summarized and calculated for adults from Odell (1932), Kennedy (1941), Copper and Fuller (1945), Rawson (1947), Martin (1952), Novakowski (1955), Webster et al. (1959), Rawson (1961), Dyer (1966), Nilsson and Svardson (1968), and Straight (1969). Juveniles were found much deeper (mean $\pm$ 95% C.I., 38.8 ± 11.5 m) than the adults (23.2 ± 4.9 m) (Table 21). The 95% confidence limits of the juvenile and adult depth distributions overlapped only by 1 m (Fig. 36).

TABLE 21. Midsummer depth and temperature distributions of juvenile and adult lake trout, from the published literature. N is the number of published observations. Does not include data for the Great Lakes.

Depth and temperature	Juveniles			Adults		
	N	Mean	95% C.I.	N	Mean	95% C.I.
Median midsummer depth (m)	13	30.8	$\pm$ 11.54	14	23.2	$\pm$ 4.89
Median midsummer temperature distribution ($^{\circ}$ C)				22	9.5	$\pm$ 1.11
Median preferred temperature determined in laboratory ($^{\circ}$ C)	7	10.2	$\pm$ 1.12			

MIDSUMMER TEMPERATURE AND DEPTH DISTRIBUTIONS OF JUVENILE AND ADULT LAKE TROUT

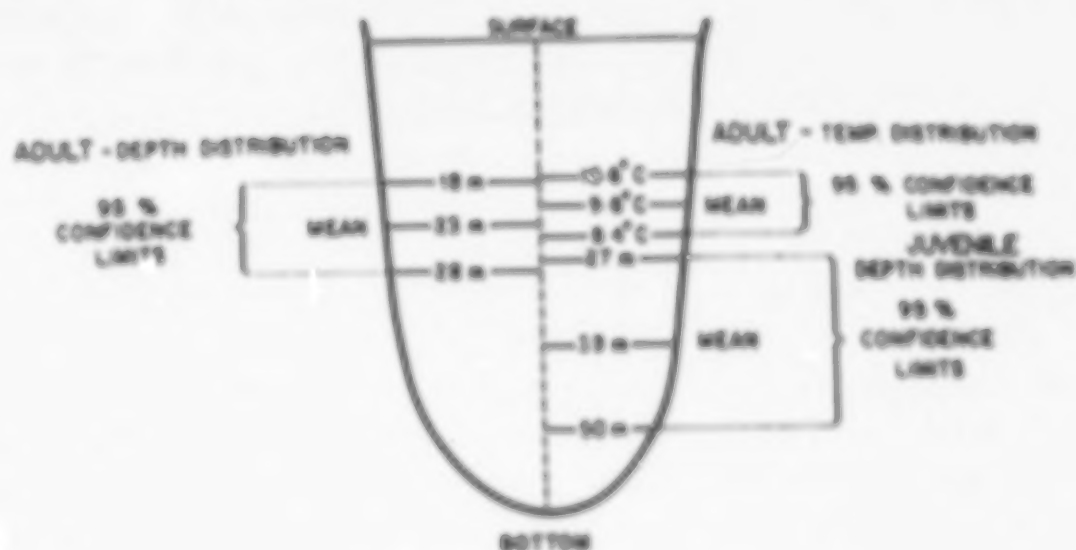


FIG. 36. Illustration of the mid- to late-summer temperature and depth preferences of juvenile and adult lake trout, as determined from the published literature.

To see if these relative depth distributions were maintained in much larger and deeper lakes, similar midsummer depth data for juvenile and adult lake trout from Great Lakes populations were compiled from literature published by Dymond et al. (1929), Tomkins (1951), Eichmeyer (1956), Van Oosten and Eichmeyer (1956), Dyer and King (1966), and Elrod and Schneider (1987). In the Great Lakes, juvenile lake trout were found in much deeper water (56.0 ± 12.2 m) than the adults (29.4 ± 9.8 m), even though both groups were found at greater depth than in inland lakes (Table 22). In these deeper lakes, the depth distributions of the two groups of lake trout showed no significant overlap.

Information about the midsummer temperature distribution of lake trout has been reported by Kennedy (1941), Cooper and Fuller (1943), Martin (1952), Rawson and Aron (1953), Nowakowski (1955), Ferguson (1958), Webster et al. (1959), Rawson (1961), Galligan (1962), Straight (1969), Johnson (1975), Martin and Ober (1980), Walsh (1980), Dahlberg (1981), Eck and Wells (1983), Marcus et al. (1984), Elrod and Schneider (1987), and Marshall et al. (1987). From these studies, the mean median temperature selected by lake trout was calculated to be $9.5 \pm 1.1^\circ\text{C}$ (Table 21), with 95% confidence limits of 8.4 to 10.6°C (Fig. 36).

Table 22. Midsummer depth distribution (m) of lake trout in the Great Lakes. Data from published literature. In most cases, lake trout were of hatchery origin.

Great lake	Juveniles		Adults	
	Range	Median	Range	Median
Superior	37-62	50	18-26	22
Michigan	55-72	59	25-30	28
	50-80	71	20-40	30
Huron (Georgian Bay)	62-128	109	17-46	42
Ontario	25-40	35	20-30	25
	36-46	41		
Mean depth (m)		56.0		29.4
95% C.I.		12.17		9.76

There were too few published data to calculate a mean midsummer temperature distribution for juvenile lake trout. However, Casselman (1987) reported that in midsummer, juvenile lake trout are normally found in deep, cold, hypolimnetic waters, which in inland lakes are approximately 4°C, but could range from 3 to 7°C. Eschmeyer (1956) and Elrod and Schneider (1987) have observed juveniles in the Great Lakes in summer at depths with median temperatures of 7.8 and 7.5°C, respectively, but ranging from 4 to 12°C. Juvenile lake trout in the Great Lakes may live in water temperatures slightly warmer than do fish from inland lakes. In inland lakes in midsummer, juveniles are found in colder, deep, hypolimnetic water, which ranges in temperature from 3 to about 5°C, well below temperatures preferred by juveniles under laboratory conditions, or selected by adults in the natural environment.

Temperature preference data, collected for juvenile lake trout under laboratory conditions by McCauley and Tait (1970), Goddard et al. (1974), Peterson et al. (1979), Mac and Bergstedt (1981), and O'Connor (1985), reveal a mean median preferred temperature of $10.2^{\circ}\text{C} \pm 1.1$ (Table 21). This is not significantly different from the mean median temperature selected by adults in the natural environment in midsummer (Table 21).

The distribution and behavioural response of lake trout in the natural environment in relation to dissolved oxygen concentration have been reported by Hoover (1937), Cooper and Fuller (1945), Rawson and Atton (1953), Paterson (1968), Carlson and Siefert (1974), Martin and Oliver (1976), and Johnson et al. (1977). From these studies, it is possible to estimate the mean median upper ($5.8 \pm 0.5 \text{ mg L}^{-1}$) and lower ($4.2 \pm 0.6 \text{ mg L}^{-1}$) oxygen response thresholds for adult lake trout (Table 23). The upper response threshold indicates the average oxygen concentration at which swimming activity initially increases in response to declining oxygen. The lower oxygen response threshold is the average oxygen concentration at which lake trout show an avoidance response.

From field and laboratory studies and from general observations of physiological response by Gibson and Fry (1954), Doudoroff and Shumway (1970), Davis (1975), and Evans (1978) for lake whitefish (*Coregonus clupeaformis*), it is possible to estimate the various low oxygen thresholds and zones for adult lake trout (Table 24). Generally, responses to low oxygen commence at 4 to 6 mg L^{-1} (approx. 30-60% saturation), with 4 down to 3 mg L^{-1} (approx. 30-20% saturation) being a limiting zone, from 3 down to 2 mg L^{-1} (approx. 20-10% saturation) an incipient lethal zone, and a lethal, or intolerable, zone of 2 mg L^{-1} or less (approx. <10% saturation).

TABLE 23. Low oxygen response thresholds for adult lake trout from summer distributions in the published literature. N is the number of published observations. Upper response threshold indicates value, at which low oxygen induced activity commences. Lower response threshold indicates values below which adult lake trout show an avoidance response.

Low oxygen response threshold	N	mg L ⁻¹	
		Mean	95% C.I.
Median upper oxygen response threshold	4	5.8	0.53
Median lower oxygen response threshold	9	4.2	0.64

TABLE 24. Low oxygen thresholds (A) and zones (B) for adult lake trout determined from field studies and general observations on physiological response from Davis (1975) and Doudoroff and Shumway (1970).

(A)

Low oxygen threshold	mg L ⁻¹	% saturation
Incipient response threshold	4.6	30-60
Incipient lethal threshold	3	20-30
Acute lethal threshold	2	10-20

(B)

Low oxygen zone	mg L ⁻¹	% saturation
Incipient limiting zone	4-3	30-20
Incipient lethal zone	3-2	20-10
Lethal (intolerable) zone	<2	<10

Categorizing lake trout summer habitat - From this summary and the published literature, it is possible to use temperature, oxygen, and depth to categorize and partition various types of lake trout summer habitat. Lake trout habitat has often been classified according to temperature and oxygen. In mid- to late summer, high temperature restricts lake trout activity from above, and low oxygen, depending on biological oxygen demand, restricts activity from the lake bottom upwards.

The habitat associated with restrictive temperature and oxygen has been variously defined and named. During summer stratification, the volume of the lake that is 10°C or less and has an oxygen concentration of 6 mg L^{-1} or more has been referred to as optimal lake trout habitat (Marcus et al. 1984; Anonymous 1987; Wilson 1988). Values from the published literature have been compiled (Tables 21 and 23), to delineate the approximate preferred habitat of adult lake trout. The volume of the lake in which the temperature is either 15.0 or 15.5°C or less and the oxygen concentration is 4 mg L^{-1} or more has been referred to as useable habitat (Anonymous 1987; Wilson 1988). According to the literature (Table 23; Martin and Olver 1976), these temperature-oxygen values approximately delineate the habitat that could be considered to be adequate and, indeed, essential, or as referred to in this study (using 15.5°C and 4.0 mg L^{-1}) the vital habitat for adult lake trout (Fig. 37).

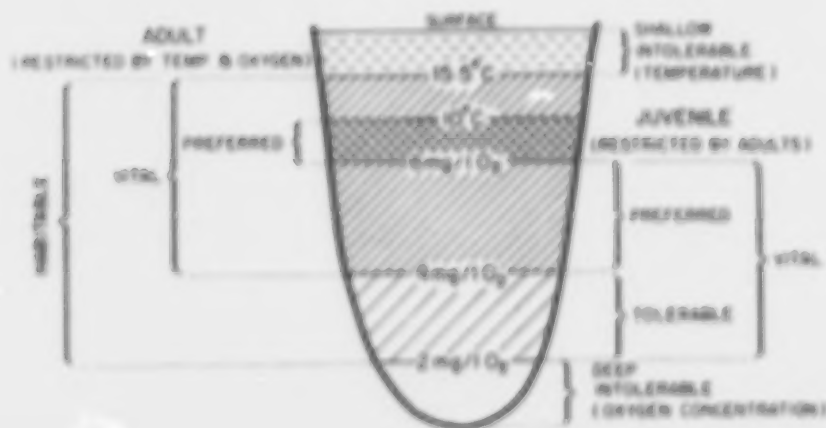


FIG. 37. Illustration of the late summer partitioning of juvenile and adult lake trout habitats, based on temperature and oxygen concentration. The shallow temperature intolerable and deep oxygen intolerable zones are also depicted.

In addition to these two general types of habitat, other categories of lake trout habitat and lake volumes were considered in the present study. They are the following portions of the lake: habitable volume - ranging from 15.5°C down to 2 mg L⁻¹ oxygen (lethal threshold); shallow temperature intolerable - warmer than 15.5°C; deep oxygen intolerable - contains less than 2 mg L⁻¹ oxygen; temperature selected by adults - ranges from 10.6°C down to 8.4°C, the 95% confidence limits about the mean selected temperature of 9.5°C (Fig. 36); depth distribution of adults - ranges from 18 to 28 m deep, the 95% confidence limits about the mean selected depth of 23.2 m; and depth distribution of juveniles - ranges from 27 to 50 m deep, the 95% confidence limits about the mean depth of 38.8 m (also the mean observational selected depth of 33 m; J.M. Casselman, unpubl. data).

Since juveniles inhabit cold, deep hypolimnetic water that is relatively homothermous and of similar temperature among lakes, during summer stagnation, dissolved oxygen would be one of the most important, and possibly even limiting, habitat variables for juveniles. The juveniles often appear to be restricted to oxygen concentrations of less than 6 mg L⁻¹ by the adults, which prefer and select concentrations greater than 6 mg L⁻¹ (Table 23), even though the oxygen requirements of juveniles are similar to those of the adults. The deep-water juvenile habitat was categorized by oxygen concentration into three broad types: preferred juvenile habitat containing from 6 to 4 mg L⁻¹ oxygen (Fig. 37); tolerable juvenile habitat containing from 4 to 2 mg L⁻¹ oxygen; and vital juvenile habitat containing from 6 to 2 mg L⁻¹ oxygen.

Summer Habitat and Lake Trout Population Status

Since it is extremely difficult to measure recruitment or the absolute abundance of juveniles, it was decided that the relative frequency of occurrence of unmarked (unclipped) lake trout from various sampling studies would provide an index of natural recruitment and be correlated with population status and general vitality of the native population. Many lake trout lakes have been stocked with hatchery fish. Since the early 1970s, most hatchery lake trout stocked by the OMNR have been fin-clipped prior to stocking. Hence, with the few exceptions considered later, most lake trout of hatchery origin can be recognized as marked (fin-clipped) fish. However, lake trout stocking has usually been conducted on need, and the amount is probably inversely correlated with the abundance of native lake trout. Hence, the relative proportion of unmarked fish in the population would be directly proportional to the relative size of the natural population and is a relative measure of recruitment success.

Lake Environment Data Base - Environmental data were acquired for 213 lake trout lakes. These excluded the Great Lakes and represented 9.2% of the lake trout lakes in Ontario. They were located in 21 OMNR administrative districts, including the Leslie M. Frost Natural Resources Centre at Dorset. The gazetteer names of these lakes, their locations, and some of their basic morphological characteristics are listed in Appendix E.

Temperature and oxygen profile data were obtained for the mid- to late-summer period, August 15 to September 20. It has been shown that temperature and oxygen conditions are most restrictive during that 5 wk period (Anonymous 1987). The temperature-oxygen profiles were measured during the 1980s, and all profiles that could be readily obtained for the 5 wk period were used. For some lakes, as many as 10 or 11 profiles were available, but the average was 2.5 ± 0.3 per lake (Appendix E). Bathymetric data were used to calculate the hypsographic volumes for each lake. The temperature-oxygen profiles and bathymetric data were obtained from OMOE, Eastern and Central Regions, and the OMNR, FAUs, District surveys, and from special studies conducted by the Research Section and the Acidic Precipitation Study Group.

Although the area of most of the lakes was less than 400 ha in area (modal class, 100 ha), some very large lakes (approx. 8.0%) were included (Fig. 38). Similarly, the majority of the lakes had a volume less than $4000 \times 10^6 \text{ m}^3$ (modal class, $1000 \times 10^6 \text{ m}^3$), but some very voluminous lakes (approx. 9.4%) were also included (Fig. 39). The modal 5 m maximum depth class for these lakes was 20 to 25 m (Fig. 40), with the majority between 15 and 45 m deep (Fig. 40). The deepest lake was 95.1 m. The frequency distributions for area, volume, and maximum depth of the lakes in this data set were similar to those in Martin and Olver (1976), indicating that these lakes were morphologically typical of Ontario lake trout lakes.

The bathymetric data were interpolated to calculate volumes at 1 m intervals. The temperature and oxygen profiles were similarly interpolated down to 1 m intervals so that the temperature and oxygen estimates were available for each of the 1 m depth volumes. Temperature was used to calculate percent oxygen saturation. These basic data were used to determine range and mean median depths, absolute and relative volumes, and mean temperature, oxygen concentration, and percent oxygen saturation for the various types of lake trout habitat zones described and defined earlier. The specific variables, the acronyms used in computer programs, and the units of measure are listed and defined in Appendix F.

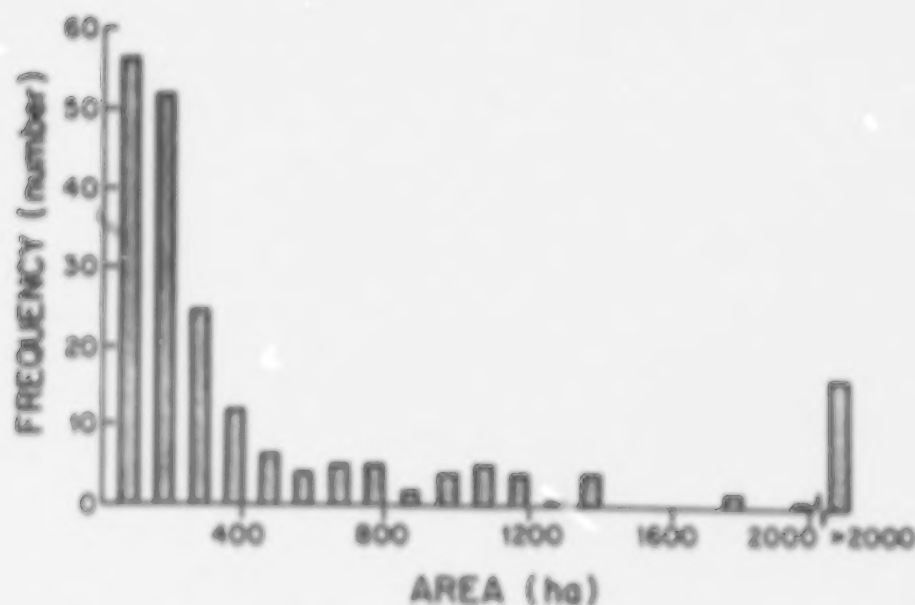


FIG. 18. Frequency distribution (number) of the area (ha) of the 212 lakes used to study available late summer lake trout habitat. Class interval is 100.

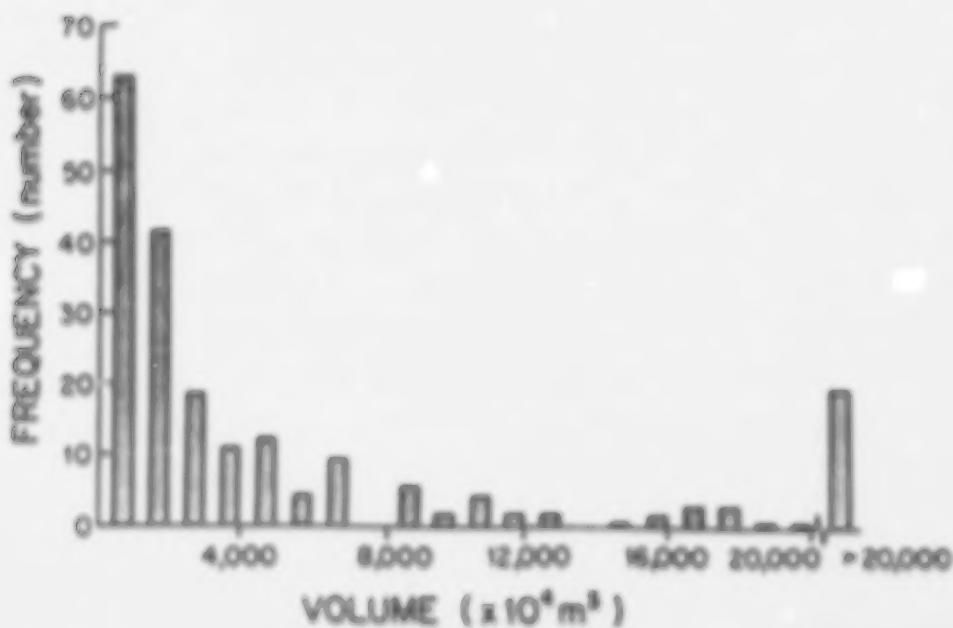


FIG. 19. Frequency distribution (number) of the volume ($\times 10^6 \text{ m}^3$) of the 212 lakes used to study available late summer lake trout habitat. Class interval is 100.

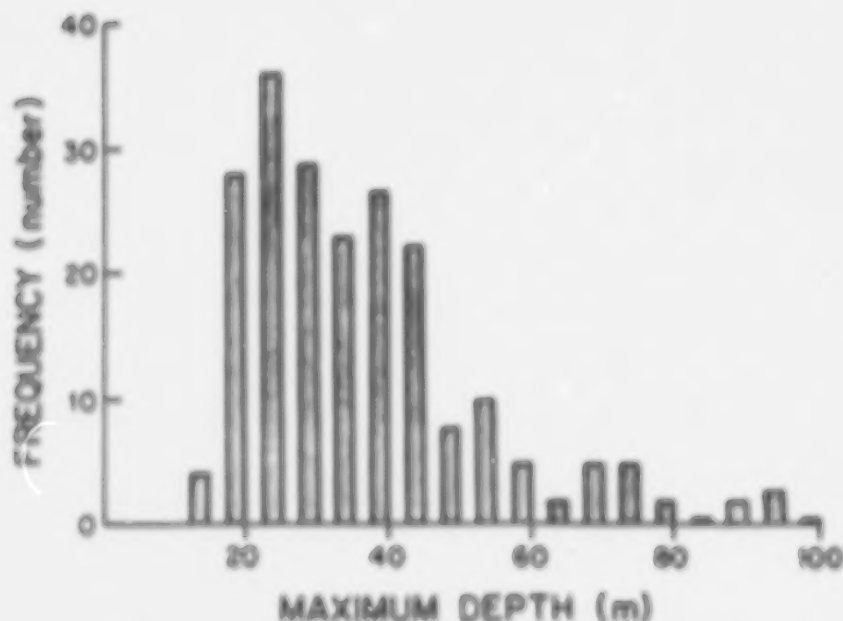


FIG. 40. Frequency distribution (number) of the maximum depth (m) of the 212 lakes used to study late summer lake trout habitat. Class interval is 5.

Lake Trout Population Data Base - A special effort was made to obtain data on lakes with broadly different population status categories (Table 1). Also included were lakes that at one time had lake trout populations which were now extinct (E) or lost (L). The population status for each of the lakes was determined from the Lake Trout Questionnaire (Lewis et al. 1990). The status of the populations was confirmed or altered during interviews that were conducted specifically to obtain additional information on relative recruitment. Nine status categories were represented in the data set. Native populations included N1, N3, N5, and N6; introduced populations included I1, I2, and I3; and extinct populations included E and L (Table 1). All categories except I3 are similar to those used in the Lake Trout Questionnaire (Lewis et al. 1990; Evans et al. 1991). Category I3 was created to parallel the N5 category and differs from I2 in that stocking was unsuccessful in producing natural reproduction, therefore the population was not self-sustaining, and stocking was discontinued.

To obtain a relative measure of natural recruitment, data were assembled on the relative occurrence of unmarked fish from various types of sampling studies such as creel census, spawning surveys, and gillnet collections. Most of the data on the incidence of fin clips were obtained from manuscripts and internal OMNR reports (e.g. Wilson 1988). However, it was necessary in some

cases, where specific data were sparse or lacking, to obtain a reasonably knowledgeable estimate from a personal-interview survey with the OMNR fisheries personnel who currently worked on the lake trout population or were responsible for its management. In a resurvey conducted some 8 mo after the original data base was assembled, to check a subset of these estimates, it was found that the two separate estimates were quite consistent, on the average within 8% of each other.

The distribution of the relative abundance of unclipped, or native, lake trout in the data set was fairly uniform (Fig. 41), except that 9.0% of the lakes contained only marked, non-native fish and 23.1% contained only unmarked lake trout.

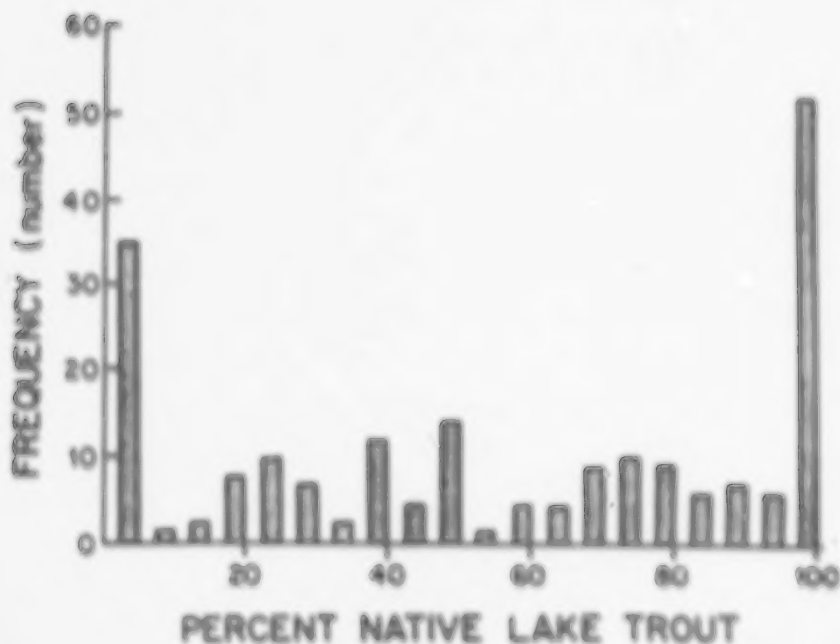


FIG. 41. Frequency distribution (number) of the relative abundance of native lake trout in 212 of the lakes used to study available late summer lake trout habitat. Class interval is 5.

For purposes of general analysis, it might be assumed that all unmarked lake trout were indigenous, although it is known that some hatchery fish are inadvertently unclipped when they are stocked, either because they have been missed or because the clip is only partial, so that the fin could eventually regenerate and the clip would be unrecognizable. Examinations of samples of fin-clipped lake trout at time of stocking in the mid 1980s in the Haliburton Highlands revealed that 8% of the "fin-clipped" hatchery lake trout were classified as "inadvertently unclipped" (J.M. Casselman, unpubl. data). It is expected that this discrepancy exists in the present data and that approximately 8% of the unclipped lake trout in stocked populations could be of hatchery origin and not naturally recruited. Therefore, a stocked lake would need to contain at least 8% unclipped lake trout before it could be said with confidence to contain any native lake trout. Therefore, we set the threshold values at 8% to indicate the presence of unmarked lake trout and at 13% to indicate a significant relative number ($> 5\%$ of population) of native lake trout.

A summary of the lake morphology data by lake trout population status (Table 25) indicated that most lakes in the data base contained native lake trout (79%). These lakes were larger and had greater volume and maximum depth than lakes in which lake trout had been introduced or had become extinct or lost.

A general comparison of the percent unmarked lake trout in the population and of population status indicated that these two variables were highly correlated (Table 25). This provided some evidence that the estimate of the percent native lake trout in the population was consistent and generally reliable and could be used in more detailed analyses. Populations that were completely self-sustaining and unstocked had only unmarked lake trout, whereas extinct and lost populations had no native fish. More importantly, populations that were natural and stocked had a higher weighted mean percentage of unmarked lake trout (57.3%) than did those which resulted from introductions (19.0%); within these two general categories, the average proportion of unmarked fish was consistent with the assessment of status (Table 25).

Analytical Procedures - When more than one profile was available for a lake, the various environmental conditions and habitat parameters were averaged. Regression analyses were conducted on the individual lake data to determine which variables showed the highest degree of correlation with the relative occurrence of unmarked, or native, lake trout. Basic statistics were calculated for each variable. The relative importance of the basic variables was examined using a chi-square test.

TABLE 25. Summary of general lake morphology, population status, and percent unmarked lake trout for the 212 lake-population data sets used in the comparative study of population status and relative occurrence of native lake trout in relation to late-summer lake trout habitat and environmental conditions. Categories of population status are defined in Table 1. N indicates populations that are native, I introduced, E extinct, and L lost.

Population status	Unmarked lake trout (%)		Lakes		Area (ha)		Volume ($\times 10^6 \text{ m}^3$)		Maximum depth (m)	
	Mean	$\pm 95\%$ C.I.	N	%	Mean	$\pm 95\%$ C.I.	Mean	$\pm 95\%$ C.I.	Mean	$\pm 95\%$ C.I.
N1	102.0		42	20	1,899	412	152.5	70.1	30.6	2.0
N3	64.2	9.1	99	43	602	234	96.0	46.5	40.7	2.0
N5	39.2	9.2	29	14	733	860	133.4	162.1	32.1	2.2
N6	31.3	75.3	4	2	1,224	2,767	264.3	703.1	41.5	30.9
I1	80.0		2	1	180		36.3		31.0	
I2	26.4	12.5	10	8	160	107	14.6	7.2	29.0	4.0
I3	2.9	5.6	15	6	198	183	15.4	9.6	20.7	2.5
E	6.0		10	5	354	502	33.4	28.6	23.2	4.1
L	0.0		3	1	155	177	9.2	14.2	17.1	4.0
Combined	56.0	11.9	212	100	635	179	98.1	53.0	36.3	2.5

For those regressions which were statistically significant ($P < 0.05$) regression analyses were conducted on equally weighted averages calculated by population status. Only seven categories were used, because data from populations that were extinct or lost were combined. Environmental conditions in lakes with populations of N6 status were not significantly different than those with populations of N5 status. Since the lakes were environmentally similar and differed only in the management decision to stock the N6 lakes with splake (*Salvelinus namaycush* $\times$ *S. fontinalis*), they were included in the N5-status lakes. In these regressions, the percent unmarked, or native, lake trout was used as the dependent variable. However, predictive regressions of X on Y were calculated to estimate the intercept values of environmental or habitat conditions that were associated with the relative occurrence of a significant number (either 8 or 13%) of unmarked, or native, lake trout.

Results - The relative occurrence of unmarked lake trout was highly correlated with many of the habitat and environmental variables selected for this study (Table 26). The habitat variables can be grouped into four general categories: preferred, vital, and habitable volumes; selected temperature distribution; mean depth and depth-range distributions for both adults and juveniles; and oxygen strata involving 2, 4, and 6 mg L⁻¹. Absolute and relative volumes and depth strata were calculated along with temperature and absolute and relative oxygen concentrations for each habitat.

The means and measures of the statistical distributions of the variables presented in Table 26 are very descriptive, since they summarize midsummer conditions in typical Ontario lake trout lakes. This data summary also indicates that in the study lakes an average of 56% of the lake trout were unmarked.

When the individual lake data were analysed, the percent of unmarked lake trout was highly significantly correlated with 53 (71%) of the 75 variables (Table 26). The variables that showed no significant correlation were not used in subsequent analyses; temperature was often included in this group.

The percent unmarked lake trout was most highly positively correlated with both absolute and relative oxygen concentrations at depths where adults (equations [30] and [31]) and juveniles (equations [39] and [40]) were usually located, the median depth (equations [14] and [21]) and depth ranges (equations [13] and [20]) of the preferred and vital habitats, and the relative size of the vital (16), preferred (9), and habitable (72) volumes (Table 26). There was a highly significant, negative, correlation between the abundance of unmarked lake trout and the volume of the lake with less than 2 mg L⁻¹ oxygen (78). Generally, these variables explained from 8 to 18% of the variation in the relative abundance of unmarked lake trout.

The highest correlation involving individual lake and population data occurred with percent oxygen saturation at the depth (18-28 m) at which adults are normally distributed (equation [37]) (Table 26). The next best correlation was with the oxygen concentration in this habitat (equation [36]). These two variables explained 16 and 17%, respectively, of the variation in the relative occurrence of unmarked lake trout.

TABLE 26. Summary of the various habitat and environmental conditions in the 212 lakes used to compare conditions in two systems for juvenile and adult lake trout, with the relative occurrence of native fish. The regression coefficients, r^2 , and P statistics are provided for relations between the occurrence of native lake trout and the listed variables using individual lake and population data. Rank indicates order of correlation for all relations for which $P < 0.05$. The population mean was individually numerically coded from 1 to 11 as indicated in Table 1.

No.	Variable	Mean	s.d.	Units	N	Median	Minimum	Maximum	Linear regression of PERUNMARK				
									Constant	Regression coefficient	r^2	P	Rank
1	DIST			No.	212	54.00	21.000	96.00					
2	POPSTATUS	4.206	2.790	No.	212	3.000		11.00	106.13	-10.420	0.637	0.000	
3	PERUNMARK	56.28	56.43	%	212	60.00		100.0					
4	NO PROFIL	2.451	1.946	N	212	2.000	1.000	11.00					
5	AREA	434.9	1299	ha	212	196.0	16.30	12220	13.54	0.004	0.022	0.009	50
6	VOLUME	9806	24790	$\times 10^3 \text{ m}^3$	212	2047	119.5	229500	54.07	0.0002	0.021	0.011	51
7	MADEP	36.34	17.44	m	212	32.00	13.33	95.10	53.24	0.637	0.092	0.000	14
8	VOLPRE	5471	11120	$\times 10^3 \text{ m}^3$	212	330.7	0.000	170000	54.05	0.0006	0.059	0.000	41
9	PERPRETOT	24.55	21.55	%	212	18.82	0.000	86.26	41.84	0.595	0.124	0.000	8
10	MTMPPRE	4.909	1.425	$^{\circ}\text{C}$	175	4.962	3.000	10.30	80.43	-2.790	0.014	0.096	
11	MOXYPRE	7.855	1.197	mg L^{-1}	175	7.755	6.000	11.57	36.91	3.123	0.012	0.124	
12	MSATPRE	41.58	9.169	% sat.	175	41.13	44.69	66.99	42.56	0.510	0.007	0.305	
13	DEFRANPRE	16.88	19.45	m	212	8.000	1.000	86.00	45.83	0.417	0.109	0.000	11
14	DEPMIDPRE	17.57	10.54	m	211	15.50	5.000	55.50	54.97	1.225	0.126	0.000	7
15	VOLVIT	4964	14200	$\times 10^3 \text{ m}^3$	212	800.0	0.000	147000	55.71	0.0005	0.061	0.000	40
16	PERVITTOT	40.35	30.35	%	212	40.14	0.000	100.0	39.18	0.670	0.140	0.000	4
17	MTMPVIT	8.309	2.051	$^{\circ}\text{C}$	208	8.007	5.762	14.65	84.78	-5.287	0.055	0.001	45
18	MOXYVIT	7.437	1.551	mg L^{-1}	208	7.470	4.000	11.72	52.95	3.295	0.020	0.016	52
19	MSATVIT	60.61	12.42	% sat.	208	60.98	52.67	94.81	42.21	0.251	0.000	0.210	
20	DEFRANVIT	25.42	19.75	m	212	19.00	1.000	91.00	63.02	0.671	0.152	0.000	6
21	DEPMIDVIT	18.65	10.34	m	212	16.00	4.000	52.67	51.53	1.596	0.144	0.000	3
22	VOLHEL	946.4	3352	$\times 10^3 \text{ m}^3$	212	115.6	0.000	52760	55.57	0.001	0.056	0.189	
23	PERHEL	4.704	4.437	%	212	5.714	0.000	57.86	54.19	0.512	0.001	0.745	
24	MTMPHEL	9.367	0.572	$^{\circ}\text{C}$	209	9.557	8.500	10.40	91.28	-3.743	0.001	0.746	
25	MOXYHEL	7.410	1.994	mg L^{-1}	209	7.200	6.107	15.01	52.98	3.180	0.062	0.000	26
26	MSATHEL	41.80	24.28	% sat.	209	40.40	1.569	125.4	55.20	0.572	0.061	0.000	29
27	DEFRHEL	2.641	4.405	m	212	1.500	1.000	47.00	54.90	0.490	0.064	0.481	
28	DEPMHEL	10.20	5.578	m	212	9.500	5.500	57.00	57.67	1.794	0.051	0.002	46
29	TMFAJIM	5.513	1.554	$^{\circ}\text{C}$	147	5.120	3.000	10.50	36.08	5.202	0.044	0.001	57
30	OSVAJIM	3.853	2.801	mg L^{-1}	149	4.500	0.100	10.00	44.24	5.551	0.001	0.000	18
31	SATAJIM	44.46	21.09	% sat.	146	46.91	0.645	82.38	42.58	0.471	0.002	0.000	15
32	MDFAJIM	21.06	1.497	m	196	21.67	16.00	22.84	45.56	7.196	0.009	0.000	17
33	VOLAJIM	1627	4445	$\times 10^3 \text{ m}^3$	212	181.6	0.000	59660	54.10	0.0014	0.028	0.005	47
34	PERAJIM	10.52	7.640	%	212	10.17	0.000	27.71	40.52	1.524	0.107	0.000	12
35	MTMPAJIM	5.570	1.424	$^{\circ}\text{C}$	196	5.415	2.555	11.15	45.48	2.224	0.006	0.224	
36	MOXYAJIM	5.174	2.067	mg L^{-1}	196	5.516	0.500	15.00	50.97	5.185	0.170	0.000	2
37	MSATAJIM	39.08	21.49	% sat.	196	41.44	0.772	83.25	50.43	0.700	0.177	0.000	1
38	TMFJIM	5.119	1.409	$^{\circ}\text{C}$	90	4.875	3.000	9.000	45.52	4.614	0.047	0.019	36
39	OSYJIM	6.458	2.552	mg L^{-1}	89	7.240	0.275	16.87	55.83	2.252	0.035	0.067	44
40	SATJIM	48.86	19.45	% sat.	82	54.56	1.972	82.38	53.06	0.545	0.046	0.022	55
41	MDFAJIM	30.96	3.050	m	141	30.42	27.00	36.56	5.06	0.776	0.027	0.025	48
42	VOLJIM	1553	4875	$\times 10^3 \text{ m}^3$	212	25.77	0.000	66050	55.40	0.0007	0.000	0.178	
43	PERJIM	5.213	7.334	%	212	1.500	0.000	29.79	50.02	1.218	0.059	0.000	31
44	MTMPJIM	5.080	1.254	$^{\circ}\text{C}$	141	4.855	2.500	8.658	50.52	2.506	0.011	0.226	

Table 26. Continued.

No.	Variable	Mean	s.d.	Units	N	Median	Minimum	Maximum	Linear regression of PERU/MCRR				
									Constant	Regression coefficient	r ²	P	Rank
45	MCNY12750	5.230	2.859	mg L ⁻¹	141	5.560	0.000	18.39	45.60	5.124	0.002	0.000	16
46	MLAT12750	36.87	21.35	% sat.	141	40.29	0.728	76.89	43.45	0.471	0.005	0.000	13
47	MDEP64	18.54	10.87	m	172	14.52	4.170	54.64	39.40	0.027	0.003	0.000	26
48	VOLUME64	682.6	2501	L/0°N	212	82.09	0.000	22960	53.56	0.001	0.003	0.347	
49	PERTU1564	8.961	9.689	%	212	3.649	0.000	42.66	59.34	-0.320	0.007	0.210	
50	MTMP64	7.579	3.366	°C	173	6.913	2.020	20.00	59.81	-0.042	0.004	0.742	
51	MCNY64	5.179	0.374	mg L ⁻¹	173	5.107	4.200	6.000	-24.86	15.006	0.026	0.013	49
52	MLAT64	40.89	4.156	% sat.	173	40.74	29.17	59.25	25.03	0.730	0.007	0.209	
53	DEPMAN64	25.12	15.90	m	173	21.00	5.000	95.00	40.18	0.000	0.004	0.000	23
54	DEPM64	16.41	10.62	m	173	13.00	3.500	54.00	45.58	0.076	0.000	0.000	40
55	MDEP62	19.12	10.99	m	181	15.56	4.472	54.64	55.96	0.014	0.076	0.000	22
56	VOLUME62	1215	4222	L/0°N	212	150.0	0.000	74000	56.24	0.00004	0.000	0.990	
57	PERTU1562	13.52	13.19	%	212	10.02	0.000	64.19	45.92	-0.565	0.002	0.000	39
58	MTMP62	7.494	3.153	°C	185	6.969	2.043	20.00	56.09	-0.002	0.013	0.007	
59	MCNY62	4.573	0.852	mg L ⁻¹	185	4.625	2.000	6.000	2.46	11.251	0.004	0.000	25
60	MLAT62	31.94	6.784	% sat.	185	36.40	17.33	59.25	4.63	1.013	0.000	0.000	30
61	DEPMAN62	26.47	15.84	m	182	20.00	0.000	94.00	55.45	0.044	0.076	0.000	20
62	DEPM62	16.22	11.05	m	182	12.00	3.500	54.00	42.90	0.002	0.004	0.001	38
63	MDEP62	19.56	10.44	m	148	17.40	4.073	56.67	55.59	0.039	0.076	0.000	32
64	VOLUME62	960.5	4652	L/0°N	212	17.52	0.000	43720	56.33	-0.0003	0.003	0.000	
65	PERTU1562	4.891	7.430	%	212	1.444	0.000	51.29	42.19	-1.251	0.003	0.000	27
66	MTMP62	6.625	2.801	°C	149	6.500	2.000	17.00	54.57	-0.009	0.002	0.790	
67	MCNY62	5.164	0.422	mg L ⁻¹	149	5.156	2.000	6.000	75.59	11.730	0.010	0.000	
68	MLAT62	24.46	3.584	% sat.	149	24.50	14.79	53.67	23.72	1.110	0.012	0.174	
69	DEPMAN62	25.20	15.40	m	150	22.50	5.500	94.00	51.54	0.073	0.001	0.000	19
70	DEPM62	16.50	10.59	m	150	16.00	5.000	56.33	36.52	0.000	0.074	0.001	4
71	PERHAB1511	46.35	33.52	%	212	33.14	0.000	99.96	57.91	0.076	0.120	0.000	9
72	VOLUME11	5171	14410	L/0°N	212	875.3	0.000	147000	55.54	0.0005	0.010	0.000	42
73	PERHAB1511	44.25	17.51	%	212	43.17	0.000	100.0	25.42	0.006	0.112	0.000	10
74	PERHAB1512	50.97	39.22	%	212	29.00	0.000	205.6	65.61	-0.200	0.007	0.000	24
75	PERHAB1517	56.86	42.37	%	212	51.83	0.000	744.3	41.89	-0.094	0.057	0.000	12
76	PERHAB1518	15.45	21.92	%	212	3.413	0.000	175.3	42.50	-0.000	0.077	0.000	21
77	PERHAB1519	24.11	21.53	%	212	16.06	0.000	100.0	60.52	-0.017	0.013	0.073	
78	VOLUME13	450.4	4594	L/0°N	212	0.000	0.000	42030	56.45	-0.0006	0.004	0.402	
79	VOLUME153	5656	17560	L/0°N	212	914.7	16.56	147000	54.01	-0.0005	0.010	0.017	15
80	PERHAB1511	8.794	17.16	%	212	0.000	0.000	100.0	45.01	-0.794	0.110	0.000	

All habitat and environmental variables used in this study could be placed in at least one of four basic categories: volume, depth, oxygen, or temperature. A test of the relative occurrence of these four basic variables indicated that they made significantly different contributions to the significant correlations (chi-square = 16.29, $P = 0.001$). Correlations involving depth were observed much more frequently (44% more) than expected when compared with the other principal variables.

Temperatures, on the other hand, were slightly under represented (21% lower), and such the results the relations were often positive rather than negative as would be expected. When depth and volume were compared separately, depth was correlated much more frequently (73% more) than expected and volume less frequently (37% lower) (chi-square = 6.6, $P = 0.011$). When oxygen and temperature were used as separate variables, oxygen provided significant correlations more frequently (18% more) than expected and temperature less frequently (61% less) (chi-square = 6.30, $P = 0.012$).

To conduct a more thorough examination of these correlations and predict their effects more precisely, the individual lake and population data were pooled by population status and averaged. Regression analysis conducted on these mean values weighted equally indicated that 16 of the original 33 pairs of correlations still showed significance ($P < 0.05$). Predictive regressions of X on Y were calculated (Table 27) to provide more precise estimates of conditions associated with the occurrence of any unmarked lake trout, enough unmarked lake trout to be confident that there were native fish present (threshold value 9% unmarked) and a significant relative number ($> 5\%$) of native lake trout (threshold value 13% unmarked).

For these average conditions, three of the highest correlations were between percent native lake trout and preferred (rank 1), vital (2), and habitable (4) volumes of the lake (Fig. 42). Predictive regressions indicated that preferred habitat was not necessary for unmarked lake trout to be present; however, a substantial volume of this habitat ($4.8 \times 10^6 \text{ m}^3$) was present when there was a significant number of native lake trout. At these levels, there was approximately twice as much vital habitat. In contrast to the preferred and vital habitat, a habitable volume of at least $1.1 \times 10^6 \text{ m}^3$ was required, if any unmarked lake trout were present (Table 27), and at least 10 times this volume if a significant number of native lake trout were present.

The slopes of these three regressions were positive and not significantly different ($P < 0.01$), indicating that the relative proportion of native lake trout in the lake increased with volume at a similar rate in these habitats even though their specific temperature-oxygen criteria were slightly different. Since these habitats represent different temperature-oxygen thresholds, together they provide the average volume-temperature-oxygen profile required to support a significant number of native lake trout.

TABLE 27. Summary of predictive regressions, coefficients, r^2 , and P statistics of comparisons between the various late summer habitat and environmental conditions (Y) and the relative occurrence of native lake trout (x). The data for lakes and populations were combined, averaged, and equally weighted by population status. The seven status categories used were N1, N3, I1, I2, and I3, and N6 combined with N5 and E and L combined. Of the 52 regressions using individual lake data that initially showed a significant correlation ($P < 0.05$ --see Rank, Table 26) with percent unmarked, or native, lake trout, this table contains the regressions of those habitat and environmental variables which, when averaged by population status, continued to show a significant ($P < 0.05$) correlation. The regressions are listed in order of decreasing significance and estimates are also provided for Y when the independent variable, percent unmarked, equalled 8 (any native lake trout) and 13 (a significant number of native lake trout).

Rank	Dependent variable	Intercept	Regression coefficient	r^2	P	Estimate when unmarked equals		Figure no.
						8%	13%	
1	Volume of preferred habitat ($\times 10^6 \text{m}^3$)	-3.006	0.597	0.88	0.001	$1.8 \times 10^6 \text{m}^3$	$4.8 \times 10^6 \text{m}^3$	42(A)
2	Volume of vital habitat ($\times 10^6 \text{m}^3$)	-0.671	0.793	0.88	0.001	$5.7 \times 10^6 \text{m}^3$	$9.6 \times 10^6 \text{m}^3$	42(B)
3	Mean percent oxygen saturation of juvenile depth distribution (27-50 m)	10.54	0.477	0.88	0.001	14.4% sat.	16.7% sat.	43(B)
4	Habitable volume ($\times 10^6 \text{m}^3$)	1.129	0.788	0.85	0.002	$7.6 \times 10^6 \text{m}^3$	$11.5 \times 10^6 \text{m}^3$	42(C)
5	Mean percent oxygen saturation of mean adult depth distribution (23 m)	17.47	0.431	0.79	0.005	20.9% sat.	23.1% sat.	44(B)
6	Mean oxygen concentration (mg L^{-1}) of juvenile depth distribution (27-50 m)	1.58	0.057	0.77	0.006	2.0 mg L^{-1}	2.0 mg L^{-1}	43(A)
7	Depth range (m) of vital habitat	8.02	0.285	0.77	0.006	10.3 m	11.7 m	46(B)
8	Mean oxygen concentration (mg L^{-1}) of mean adult depth distribution (23 m)	2.38	0.056	0.76	0.007	2.8 mg L^{-1}	3.1 mg L^{-1}	44(A)
9	Median depth (m) of preferred habitat	9.26	0.153	0.76	0.007	10.5 m	11.3 m	47(A)
10	Median depth (m) of vital habitat	10.16	0.162	0.76	0.008	11.5 m	12.3 m	46(A)
11	Mean percent oxygen saturation of adult depth distribution (18-28 m)	16.46	0.425	0.74	0.009	19.9% sat.	22.0% sat.	45(B)
12	Mean oxygen concentration (mg L^{-1}) of adult depth distribution (18-28 m)	2.19	0.055	0.71	0.012	2.6 mg L^{-1}	2.0 mg L^{-1}	45(A)
13	Depth range (m) of preferred habitat	3.30	0.254	0.71	0.014	5.3 m	6.6 m	47(B)
14	Maximum depth (m)	24.47	0.234	0.64	0.024	26.3 m	27.5 m	48
15	Volume of adult depth distribution (18-28 m ($\times 10^6 \text{m}^3$))	0.745	0.246	0.62	0.024	$2.7 \times 10^6 \text{m}^3$	$4.0 \times 10^6 \text{m}^3$	
16	Mean percent oxygen saturation of volume of lake with oxygen concentration of 2-6 mg L^{-1}	32.63	0.061	0.64	0.026	33.1% sat.	33.4% sat.	
17	Median depth (m) of adult selected temperature distribution	8.87	0.026	0.62	0.028	9.1 m	9.2 m	

TABLE 27. Continued

Rank	Dependent variable	Intercept	Regression coefficient	r^2	P	Estimate when unmarked equals		Figure no.
						8%	13%	
18	Volume of preferred habitat as a percent of volume of vital habitat	23.15	0.470	0.61	0.028	26.9%	29.3%	
19	Volume of lake with oxygen concentration of 2-4 mg L ⁻¹ as a percent of total volume	8.71	-0.073	0.61	0.029	8.1%	7.8%	49(A)
20	Volume of lake with oxygen concentration <2 mg L ⁻¹ as a percent of total volume	22.26	-0.258	0.61	0.029	20.2%	18.9%	49(B)
21	Mean depth of adult depth distribution (18-28 m)	19.66	0.027	0.58	0.037	19.9 m	20.0 m	
22	Mean oxygen concentration of volume of lake with oxygen concentration of 4-6 mg L ⁻¹	5.09	0.002	0.55	0.045	5.1 mg L ⁻¹	5.1 mg L ⁻¹	
23	Habitable volume as a percent of total volume of the lake	31.80	0.253	0.55	0.047	33.8%	35.1%	49(C)
24	Temperature of mean adult depth distribution (23 m)	4.39	0.014	0.55	0.047	4.5°C	46°C	50

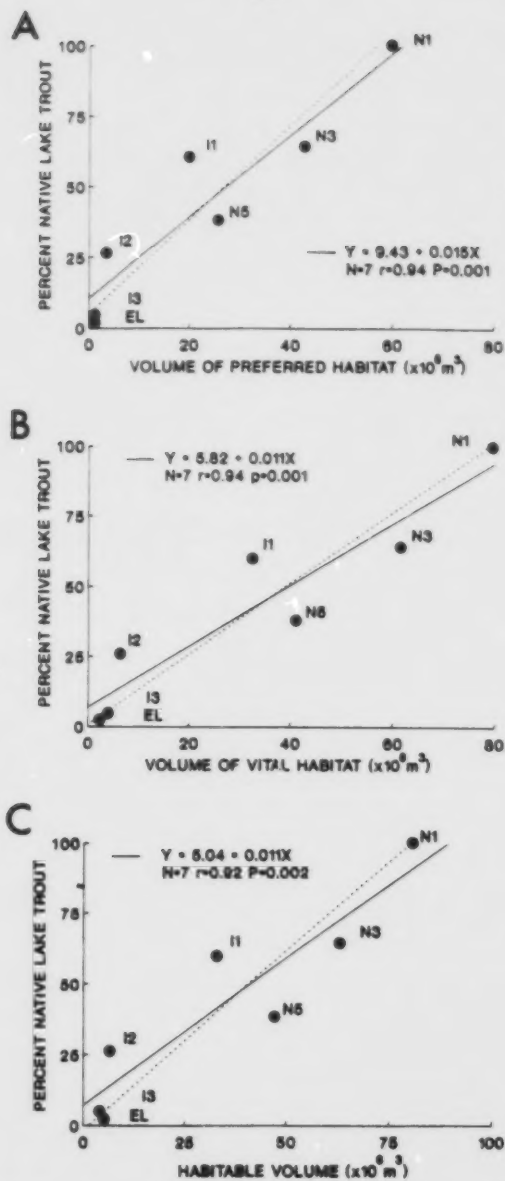


FIG. 42. Relations between percent native lake trout and (A) volume ($\times 10^6 \text{ m}^3$) of the preferred habitat ($< 10^\circ \text{C}$ and $> 6 \text{ mg L}^{-1}$ oxygen), (B) volume ($\times 10^6 \text{ m}^3$) of the vital habitat ($< 15.5^\circ \text{C}$ and $> 4 \text{ mg L}^{-1}$ oxygen), and (C) the amount of habitable ($< 15.5^\circ \text{C}$ and $> 2 \text{ mg L}^{-1}$ oxygen) volume ($\times 10^6 \text{ m}^3$) in the lake. Dashed lines illustrate the predictive regression of X on Y. The relations were constructed from equally weighted means for each population status. The alpha-numeric codes beside the data points indicate lake trout population status (Table 1). N indicates native lake trout populations and I indicates introduced populations. N5 is a combined status including N5 ($n = 29$) and N6 ($n = 4$). EL combines extinct E ($n = 10$), and lost populations, L ($n = 3$).

The abundance of native lake trout was also highly correlated with absolute (rank 3) and relative (rank 6) oxygen concentrations at depths (27-50 m) normally occupied by juvenile lake trout (Fig. 43). These correlations were positive, and the predictive regressions indicated that at least 2.0 mg L⁻¹ oxygen and 14% oxygen saturation were required before any unmarked lake trout were present and at least 2.3 mg L⁻¹ oxygen and 17% oxygen saturation would be required for a significant number of native lake trout to occur (Table 27; Fig. 43).

Similar highly significant positive correlations were obtained with mean oxygen concentration at the mean depth (23 m) (Fig. 44) and depth distribution (18-28 m) (Fig. 45) at which adults were normally found (rank 8 and 12, respectively, (Table 27)). For unmarked lake trout to occur, oxygen concentration and saturation values for these two depth variables were at least 2.8 mg L⁻¹ and 21% saturation and 2.6 mg L⁻¹ and 20% saturation respectively (Table 27). From these relationships, it is estimated that at least 3.1 mg L⁻¹ oxygen and 23% oxygen saturation and 2.9 mg L⁻¹ oxygen and 22% saturation, respectively, would be required for a significant number of native lake trout to be present.

The relative number of native lake trout in the lake was highly significantly and positively correlated with both the median depths and depth ranges of the vital (Table 27, ranks 10 and 7; Fig. 46) and preferred (Table 27, ranks 9 and 13; Fig. 47) habitats. Predictive regressions indicated that substantial bands of vital habitat 12 m deep, at a median depth of approximately 12 m, and preferred habitat 7 m deep, at approximately 11 m, were required for a significant number of native lake trout to be present (Table 27). These depth estimates delineate the volumes estimated earlier.

There was a direct relationship between the relative numbers of native lake trout and the maximum depth of the lake (Fig. 48). However, predictive regressions indicated that lakes shallower than 26.3 m would not have significant numbers of unmarked lake trout (Table 27, rank 14; Fig. 48). Indeed, lakes where populations had been lost or where introductions had been unsuccessful were shallower than this critical depth (Table 25), and most lakes that had populations which had become extinct were also shallower. From the predictive regression of *X* on *Y*, it was estimated that on the average lakes had to be at least 27.5 m deep before there would be significant numbers of native lake trout (Table 27, rank 14). This depth estimate is remarkably similar to the upper limits of the depth distribution of juvenile lake trout, calculated from the published literature and ranging from 27 to 50 m.

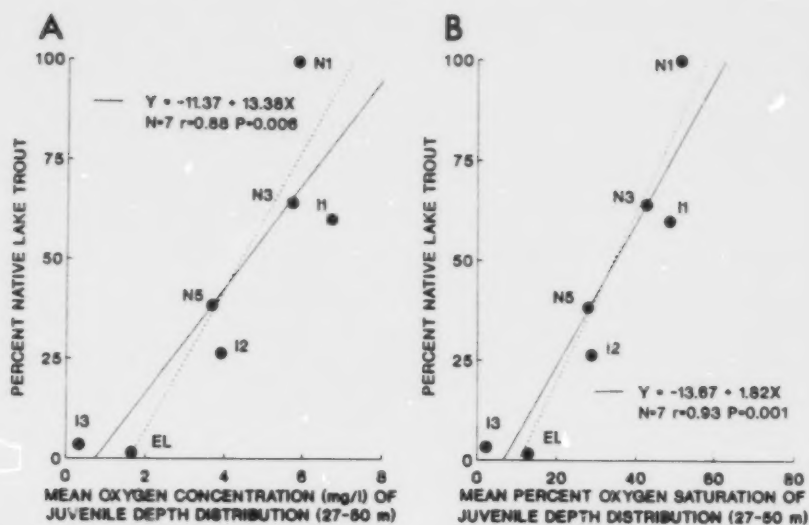


FIG. 43. Relations between percent native lake trout and (A) mean oxygen concentration (mg L^{-1}) and (B) mean percent oxygen saturation of the published depth distribution (27-50 m) of juvenile lake trout. Dashed lines illustrate the predictive regression of X on Y. The relations were constructed from equally weighted means for each population status. The alpha-numeric codes beside the data points indicate lake trout population status (Table 1). N indicates native lake trout populations and I indicates introduced populations. N5 is a combined status including N5 ($n = 29$) and N6 ($n = 4$). EL combines extinct, E ($n = 10$) and lost populations, L ($n = 3$).

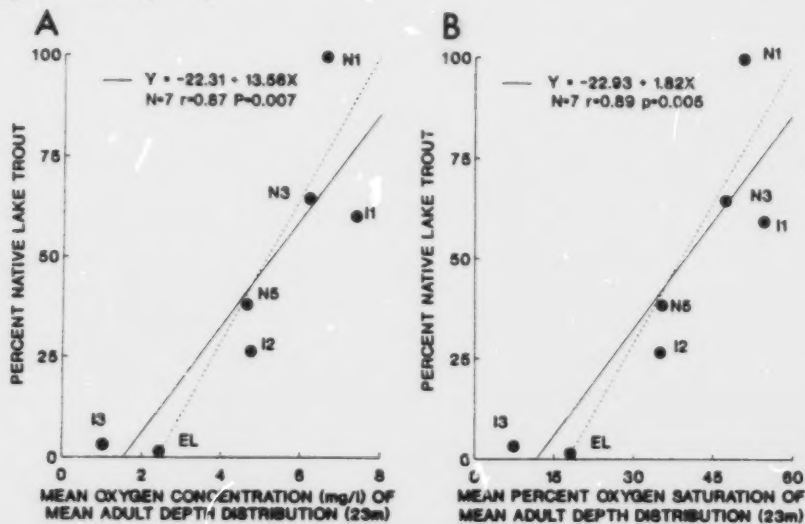


FIG. 44. Relations between percent native lake trout and (A) mean oxygen concentration (mg L^{-1}) and (B) mean percent oxygen saturation of the published mean depth distribution (23 m) of adult lake trout. Dashed lines illustrate the predictive regression of X on Y. The relations were constructed from equally weighted means for each population status. The alpha-numeric codes beside the data points indicate lake trout population status (Table 1). N indicates native lake trout populations and I indicates introduced populations. N5 is combined status including N5 ($n = 29$) and N6 ($n = 4$). EL combines extinct, E ($n = 10$), and lost populations, L ($n = 3$).

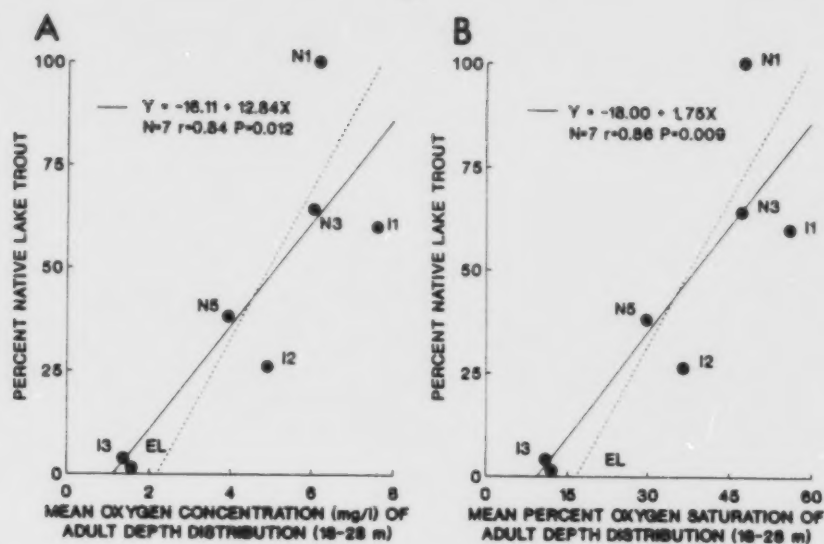


FIG. 45. Relations between percent native lake trout and (A) mean oxygen concentration (mg L^{-1}) and (B) mean percent oxygen saturation of the published depth distribution (18-28 m) of adult lake trout. Dashed lines illustrate the predictive regression of X on Y. The relations were constructed from equally weighted means for each population status. The alpha-numeric codes beside the data points indicate lake trout populations status (Table 1). N indicates native lake trout populations and I indicates introduced populations. N5 is a combined status including N5 ($n = 29$) and N6 ($n = 4$). EL combines extinct, E ($n = 10$), and lost populations, L ($n = 3$).

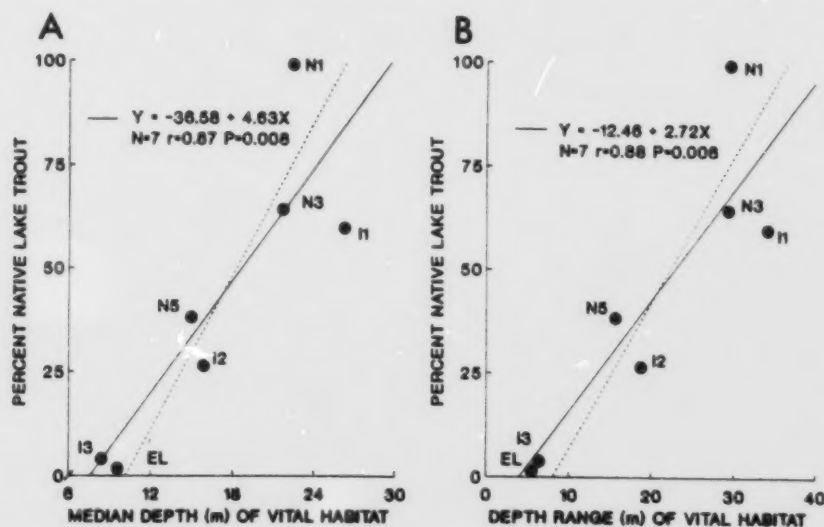


FIG. 46. Relations between percent native lake trout and (A) median depth (m) and (B) depth range (m) of the vital habitat ($<15.5^{\circ}\text{C}$ and $>5 \text{ mg L}^{-1}$ oxygen). Dashed lines illustrate the predictive regression of X on Y. The relations were constructed from equally weighted means for each population status. The alpha-numeric codes beside the data points indicate lake trout population status (Table 1). N indicates native lake trout populations and I indicates introduced populations. N5 is a combined status including N5 ($n = 29$) and N6 ($n = 4$). EL combines extinct, E ($n = 10$), and lost populations, L ($n = 3$).

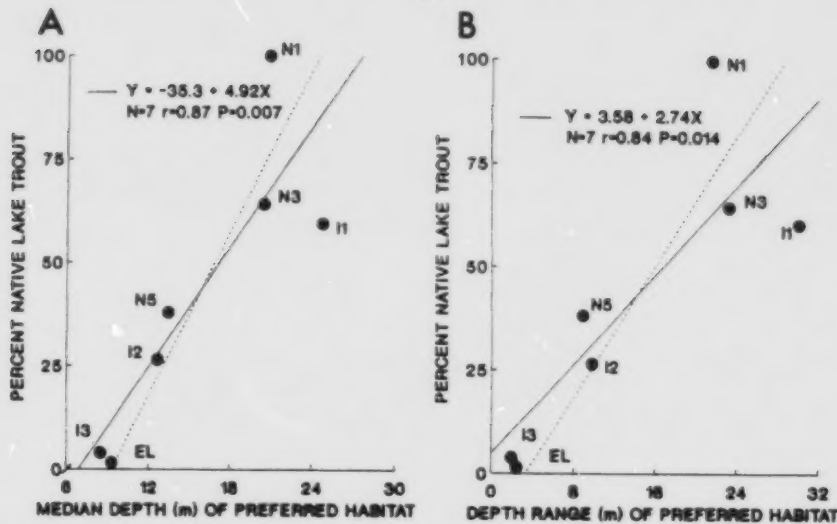


FIG. 47. Relations between percent native lake trout and (A) median depth (m) and (B) depth range (m) of the preferred habitat ($<10^{\circ}\text{C}$ and $>6\text{ mg L}^{-1}$ oxygen). Dashed lines illustrate the predictive regression of X on Y. The relations were constructed from equally weighted means for each population status. The alpha-numeric codes beside the data points indicate lake trout population status (Table 1). N indicates native lake trout populations and I indicates introduced populations. N5 is a combined status including N5 ($n = 29$) and N6 ($n = 4$). EL combines extinct, E ($n = 10$), and lost populations, L ($n = 3$).

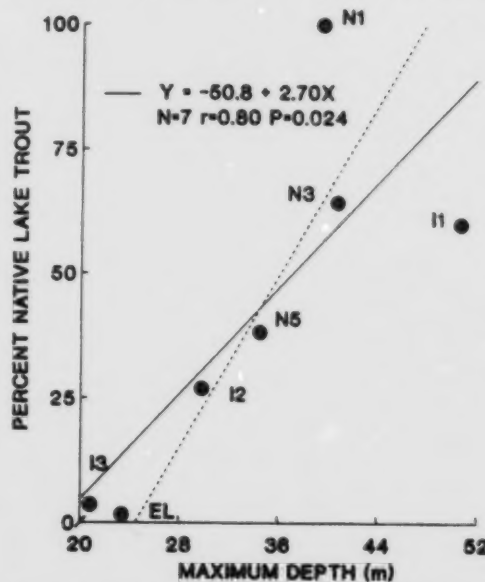


FIG. 48. Relation between percent native lake trout and maximum depth (m) of the lake. Dashed line illustrates the predictive regression of X on Y. The relation was constructed from equally weighted means for each population status. The alpha-numeric codes beside the data points indicate lake trout population status (Table 1). N indicates native lake trout populations and I indicates introduced populations. N5 is a combined status including N5 ($n = 29$) and N6 ($n = 4$). EL combines extinct, E ($n = 10$), and lost populations, L ($n = 3$).

Three important relative volumes were correlated with the occurrence of native lake trout (Fig. 49). Two of these involved the amount of low-oxygen water, including the 2 to 4 mg L⁻¹ oxygen stratum and the volume of the lake with less than 2 mg L oxygen. In both cases, the percent native lake trout was negatively related to low oxygen conditions. It is estimated that if more than 8% of the volume of a lake trout lake (Table 27, rank 19) has an oxygen concentration from 2 to 4 mg L⁻¹, the number of native lake trout present will be insignificant. The same would be true if more than approximately 19% of the lake volume contained less than 2 mg L⁻¹ oxygen. The percent of unmarked, or native, lake trout was directly correlated with the amount of habitable volume of the lake (Fig. 49C). And it was estimated that if the habitable volume were less than approximately 35% of the total volume of the lake (Table 27), the lake would not contain a significant number of native lake trout.

The specific volumes, depths, and oxygen conditions associated with these correlations and predictive regressions could be combined to describe and model the threshold habitat and environmental conditions that would be associated with the occurrence of significant numbers of native lake trout (Table 27, 13% unmarked).

The correlation between the percent native lake trout and temperature of the mean adult depth distribution (23 m) was just barely significant ($P = 0.047$, Fig. 50). This correlation was positive, which seems paradoxical, because it would predict that if the deeper waters were warmer, there would be more native lake trout (Table 27). Even though these temperature differences were small, the results suggest that slight increases in temperature below the preferred zone would enhance lake trout production.

Discussion and Conclusions

The factors that affect the size of a native lake trout population and natural recruitment are complex and interactive, and no single habitat or environmental variable would be expected to act completely in isolation. However, an examination of the variables that were highly correlated with the relative abundance of native lake trout could help to provide useful insights.

The quantity and quality of adult lake trout habitat appear to be important determinants of the production of native lake trout. There are many ways that this habitat could affect natural native

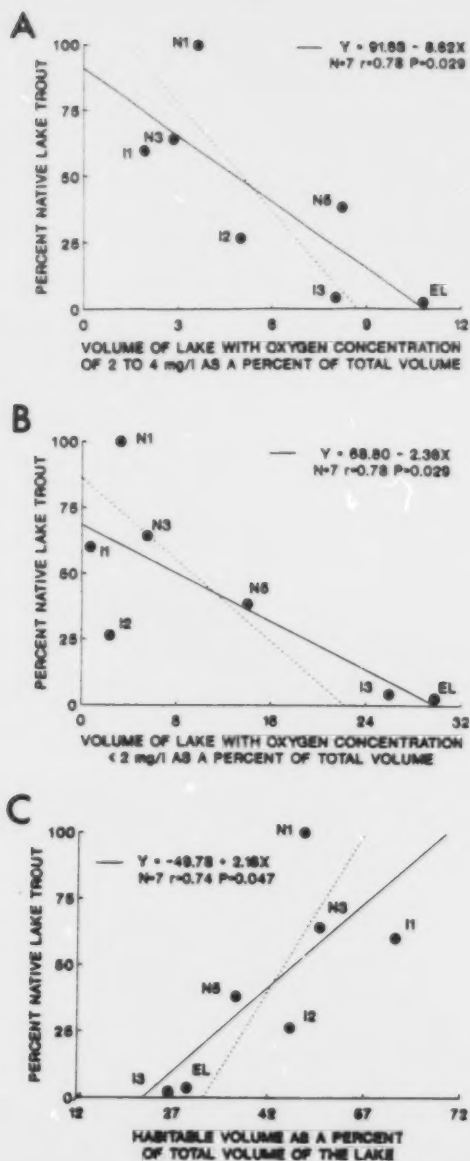


FIG. 49. Relations between percent native lake trout and (A) volume of the lake with an oxygen concentration of from 2-4 mg L⁻¹ as a percent of the total volume of the lake, (B) volume of the lake with an oxygen concentration <2 mg L⁻¹ as a percent of the total volume of the lake, and (C) habitable volume (<15.5°C and >2 mg L⁻¹ oxygen) as a percent of total volume of the lake. Dashed lines illustrate the predictive regression of X on Y. The relations were constructed from equally weighted means for each population status. The alpha-numeric codes beside the data points indicate lake trout population status (Table 1). N indicates native lake trout populations and I indicates introduced populations. N5 is combined status including N5 ($n = 29$) and N6 ($n = 4$). EL combines extinct, E ($n = 10$), and lost populations, L ($n = 3$).

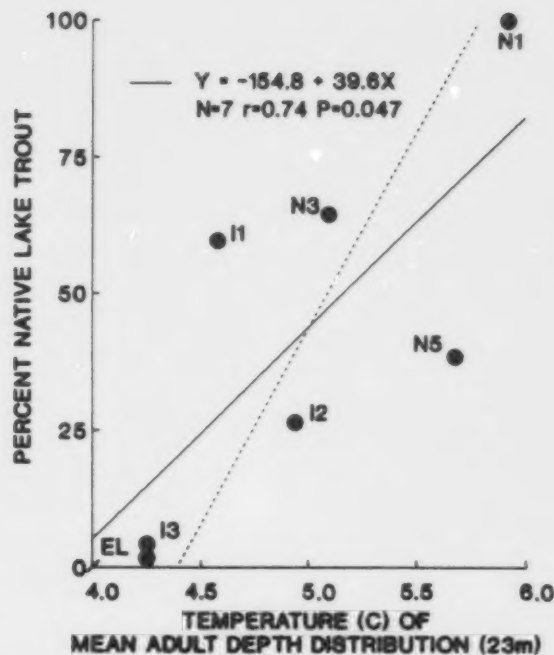


FIG. 50. Relation between percent native lake trout and temperature ($^{\circ}\text{C}$) of the published mean depth distribution (23 m) of adult lake trout. Dashed line illustrates the predictive regression of X on Y. The relation was constructed from equally weighted means for each population status. The alpha-numeric codes beside the data points indicate lake trout population status (Table 1). N indicates native lake trout populations and I indicates introduced populations. N5 is a combined status including N5 ($N = 29$) and N6 ($n = 4$). EL combines extinct, E ($n = 10$), and lost populations, L ($n = 3$).

production of lake trout. More habitat would provide a greater spatial separation of adults, reducing intraspecific interaction and making small fish less vulnerable to cannibalism. If more adult habitat is available, it would allow the large fish to disperse more widely, making them less vulnerable to normal angling pressure and could simply provide for a larger adult population. This would produce a larger number of mature fish and increased potential for natural reproduction and recruitment. Increased adult habitat also indicates a greater reservoir of cold water and associated higher oxygen concentrations throughout the water column. This would extend into deep water and be correlated with an increase in the quantity and quality of the juvenile nursery habitat.

The amount of oxygen in deep water was directly associated with the relative abundance of native lake trout and natural recruitment especially when associated with the deeper waters (27-50 m) that juveniles normally occupy. Concurrently, if the shallower portions of the lake, which are normally occupied by adults, do not contain at least 2.9 to 3.1 mg L⁻¹ oxygen, then there may not be a significant number of native fish and natural recruitment may not occur. These oxygen values agree very closely with the incipient lethal low oxygen threshold (3 mg l⁻¹; Table 24) used to establish criteria for the various habitat and environmental conditions. The amount of oxygen with depth is especially important, since it determines the quantity and quality of the habitat that is available. Any factor that causes a decrease in the hypolimnetic oxygen concentration below the lower and upper incipient response thresholds (4-6 mg L⁻¹) would reduce not only the amount of adult habitat but also the juvenile habitat, and the size of the native lake trout population.

This conclusion is supported by the correlation which indicated that the relative amount of poorly oxygenated deep water was inversely related to the occurrence of native lake trout. Indeed, if the deep hypolimnetic waters did not contain more than approximately 2.3 mg L⁻¹ (Table 27) with an oxygen saturation of approximately 17%, juvenile lake trout could not survive and a self-sustaining lake trout population would not be possible. It appears that juveniles can tolerate lower oxygen concentrations than adults, which might reduce their activity and growth. Nevertheless, as the oxygen concentration decreases, the quality of the juvenile habitat that is available would decrease, restricting their distribution and forcing them to move out of the deeper, less oxygenated water. This would tend to force the juveniles into greater proximity with the adults, making them more vulnerable to cannibalism.

Depth of the lake was one of the most important single variables directly associated with relative occurrence of native lake trout. This variable provided direct evidence that under average conditions, lakes must be at least 27 m deep if a significant number of native lake trout are to be present. An alternative explanation for this result is that the relative size of the native lake trout population is simply inversely related to stocking rate, which is often in direct proportion to exploitation pressure. It could be further argued that larger, deeper lakes have relatively less exploitation pressure, hence are less heavily stocked. In this case, relative abundance of native lake trout, therefore, might not be related to recruitment associated with depth, oxygen, and quantity and quality of the nursery habitat. Over the size range of the lakes examined, however, stocking does not appear to explain the

differences observed in the relative occurrence of native lake trout with habitat volumes, depths, or oxygen concentration. Although the percent of unmarked lake trout was correlated with lake area and volume, these variables explained only 2% of the variation in the relative abundance of unmarked lake trout (Table 26) and were not correlated with the presence of native fish when values averaged by population status were examined. The combined effects of stocking and exploitation rate might be important, because stocking rates and exploitation rates are higher in small lakes. The low correlation with lake size, however, suggests that the relative abundance of native fish is primarily dependent on lake trout production capacity of the lakes rather than on rates of stocking or exploitation. The effects of stocking and exploitation on the relative abundance of native lake trout is examined in detail later in this report (p. 123, 127).

Generally, summer temperatures in the deeper waters of temperate-region oligotrophic lakes at this latitude neither affect survival nor appear to have an adverse effect on growth of lake trout. Temperature was generally not well correlated with the relative occurrence of native lake trout, although temperature is a critical component of the preferred and vital habitats which were highly significant predictors. Temperature appears to be less important, therefore, than depth and oxygen in affecting the abundance and possibly natural recruitment of native lake trout.

Maximum depth is an important variable, and the estimates associated with it are quite specific. However, the correlation and predictive regressions depict average conditions. Therefore, there are some rather notable exceptions. There are shallow lakes that have never been stocked and contain self-sustaining native lake trout. In fact, 10 (25%) of the N1 population status lakes (lakes that contain native populations with natural reproduction and are self-sustaining and unstocked) were shallower than would be considered necessary to produce a significant number of native lake trout. This is not surprising, because many factors could influence these exceptions. For example, two (Little Black and Stocking) and possibly three of these 10 lakes are known to contain lake trout that are genetically different from other Ontario lake trout (P.E. Ihssen, OMNR, Box 5000, Maple, Ont. L6A 1S9 and J.M. Casselman, unpubl. data). The adults of this genotype behave quite differently than other Ontario lake trout: they are more strongly pelagic, they range more widely through the water column, and they appear to be less restricted by temperature (J.M. Casselman, unpubl. data). Also, another group of these lakes is in northwestern Ontario, where the summer surface waters could be cooler and less restrictive, allowing the adults to occupy shallower water. Lakes in another

set are quite small and in a region that is relatively undeveloped. The thermocline might be shallower and the deep waters more highly oxygenated. No doubt the morphology of the deep basin of the lake would also affect the amount of deep-water habitat that is available.

Although these explanations are speculative, they indicate that a more detailed analysis of additional covariants is required if the relations are to be refined and the exceptions fully explained. A more thorough understanding of the other habitat and environmental components, along with the environmental requirements and behaviour of the juveniles and adults, would no doubt improve our understanding of these correlations. Indeed, if the adult population is small, size-selective predation pressures would not be as great; therefore the juveniles could range more widely and depth constraints on the juveniles would be less important.

Additional analyses to refine and improve these relationships would, however, require a more direct and accurate estimate of the size of the native lake trout population. Approximately 12% of the lakes with a lake trout population of an N3 status were shallower than would be considered necessary to contain any native lake trout. Some of these exceptions might be explained by the fact that the estimate of the relative occurrence of native lake trout was in some cases only approximate; therefore, it could be imprecise and in some cases possibly inaccurate.

It is apparent that the relative occurrence of native lake trout and natural recruitment are correlated with the amount of oxygen in deep water and with the maximum depth of the lake. The amount of available oxygen in the deep-water nursery habitat ($>2.3 \text{ mg L}^{-1}$) will affect the abundance of juveniles, because of the effect of limiting oxygen on scope for activity, feeding and growth (Davis 1975) and, in turn, on recruitment, production, and the size of the native lake trout population. Indeed, the amount of deep-water nursery habitat may be one of the single most important factors affecting the productivity of lake trout populations. As has been indicated, juvenile lake trout use this habitat, depending upon growth rate, for up to 2 to 4 yr (J.M. Casselman, unpubl. data). Hence, several age groups and sizes occupy this critical volume at the same time. Density-dependent, size-selective predation and mortality no doubt operate among the juveniles within the deep-water nursery habitat, since the habitat is restricted and lake trout generally are strongly piscivorous. Depending upon the size of the nursery habitat, this density-dependent mechanism could regulate the number of juvenile lake trout available to be recruited as sub-adults (see p. 104).

For most lakes in the data set, the volume of the juvenile habitat was small, especially if the lakes were shallow. For lakes in this data set that were deep enough to have juvenile habitat (27-50 m deep), there was a highly significant positive correlation between the volume of this juvenile habitat relative to the entire volume of the lake (RV--%) and maximum depth (MD--m):

$$RV = -9.54 + 0.39MD$$

$$N = 141, r = 0.828, P = 0.000$$

where $RV = (\text{volume of the juvenile habitat} / \text{total volume of the lake}) \times 100$

It can be estimated from this relationship that a lake which is just deep enough to have a significant number of native lake trout (maximum depth 27.5 m) would have 1.2% of its total volume as juvenile habitat. In this lake set, 50% of the lakes had a juvenile habitat that was less than 6% of the total lake volume, and in 21% of the lakes, less than 1%. The actual ability of a lake to produce and maintain a lake trout population is best understood in terms of habitable and vital volumes. Since lake trout are restricted by temperature in midsummer, it is appropriate to estimate the volume of the juvenile habitat as a percent of the habitable volume, rather than total lake volume, to appreciate the significance of its relative importance. The average volume of the juvenile habitat among lakes was 24% of the habitable volumes which averaged 44% of total volume.

Both relative and absolute size of the juvenile habitat are critically important, since once the thermocline becomes established, this is the portion of the lake that is most susceptible to oxygen depletion and resulting environmental degradation. These act to reduce the size and quality of the juvenile habitat. This juvenile habitat is especially critical because the entire lake trout production depends upon it, with several juvenile age groups using it at one time. The size of the habitat available to the adults is very much greater (preferred 75% and vital 96% of the habitable volume) and is less critical because the adults, although larger in size, can range more widely and theoretically may be fewer in number, since this habitat needs to support only enough sub-adults and adults to meet the reproductive needs of the population. Not only is the juvenile habitat critically important for natural production, but hatchery-stocked juveniles also live in this refugium, and if stocking is heavy, the introduced trout could be significant competitors and predators of the native fish.

In support of our original hypothesis, the results suggest that the quantity and oxygen content of the juvenile habitat are major factors directly affecting the natural recruitment and occurrence of native lake trout. Since anthropogenic eutrophication would affect hypolimnetic oxygen depletion,

it could directly limit native lake trout production through its effect on the quantity and quality of the juvenile habitat, which even under entirely natural conditions may limit and restrict native lake trout abundance and productivity, depending on lake morphometry and productivity.

THE CANNIBALISM-RECRUITMENT HYPOTHESIS

There is some evidence to suggest that cannibalism is an important feature of the dynamics of lake trout populations. First, cannibalism in lake trout has been reported in wild populations (Martin and Olver 1980). Second, juvenile lake trout segregate from the adults during summer thermal stratification of the water column (Tables 21 and 22), and third, stocked lake trout juveniles appear to be more vulnerable to cannibalism (Martin and Olver 1980), probably due to their tendency to occupy shallow water for a period of time following release. We suggest that cannibalism is an emergent expression of an important regulatory mechanism in lake trout populations.

Johnson (1976) concluded that cannibalism may play a suppressive role in regulating recruitment of juvenile lake trout into the adult stock in Arctic lakes, but that confinement of juveniles to the peripheral habitats, along shorelines and tributary streams, is the key factor making them vulnerable to other primary causes of mortality. Confinement of juveniles to the deep hypolimnion of more southern lakes would seem to be a homologous behaviour. The risk of predation by other species, and the inhospitable thermal conditions in the littoral habitats of southern lakes during summer, precludes their use by juvenile trout during that season. We propose, however that cannibalism or the risk of cannibalism is the primary mechanism of intraspecific population regulation in lake trout. Even in southern lakes where the incidence of cannibalism seems to be quite low (Martin 1970), we suggest that the annual mortality of juveniles due to cannibalism is important. The mechanism that we hypothesize has major implications for production of lake trout in Ontario lakes, potentially explaining the critical production bottleneck in marginal habitats. Also, in lakes degraded by nutrient enrichment and associated oxygen depletion of the hypolimnetic zone, production would be expected to be compromised, either due to the lethality of the physical conditions, or to elevated juvenile mortality resulting from forced association of juveniles and adults, as the young fish avoid low oxygen conditions during late summer.

Lake Trout Cannibalism in Lake Opeongo

Based on estimates of lake trout population size in Lake Opeongo and the incidence of cannibalism, it is possible to estimate the magnitude of the mortality of juveniles caused by intraspecific predation. The average standing stock of adult trout aged 6 yr and greater, from 1936 to 1965, was 5033 (B.J. Shuter, OMNR, Box 5000, Maple, Ont. L6A 1S9, unpubl. data), and the incidence of juvenile lake trout in adult lake trout stomachs was 0.00064 (11 trout in 17,171 stomachs examined) during the same period (Martin 1970). Hypothetically, if the time required to digest a juvenile lake trout is about 24 h, and each adult lake trout eats one juvenile during the 150 d survey period, the probability of a juvenile lake trout in the stomach of an adult would 0.0067 because, on any given day, 33.55 (i.e. $5033/150$) trout would have a juvenile in their stomach and the probability of sampling one of those fish would be $33.55/5033$ (i.e. 0.0067). This sampling probability is only true, however, if the likelihood of sampling trout is independent of their level of satiation. Since most of the fish were sampled by angling, this is unlikely to be true. In Martin's (1970) study, only 59.6% of the trout examined had fish prey in their stomachs. The expected probability of finding a juvenile trout in the stomach of an adult, therefore, is only 0.0040 (i.e. 0.0067×0.596), because of the likelihood of sampling fish that had empty stomachs. The actual observed incidence of cannibalism is 0.00108 for trout that had fed on fish, therefore, the number of lake trout juveniles eaten by each adult trout, from May to September, which is the period of the population and stomach analysis surveys, is 0.27 (i.e. $0.00108/0.0040$).

The total number of juvenile trout eaten during the survey period, therefore, is 1359 (i.e. 5033×0.27). A simple linear expansion of this estimate to the entire year suggests a total annual consumption of 3262 juvenile trout. Diet studies by Martin (1970) indicate that the percentage of lake trout with fish of all species in their stomachs is highest during the winter months, which represent only 10% of the observations in the data set. It is possible, therefore, that predation on lake trout is higher during times of the year not covered by the survey, although we would expect reduced feeding activity at colder temperatures characteristic of the winter months, which might counteract the influence of a seasonal shift to a more piscivorous diet. Given these uncertainties, we have opted to apply a linear extrapolation to obtain an annual estimate of total juvenile trout consumed (i.e. 3262 juveniles).

The actual estimate of the incidence of cannibalism is assumed to be a conservative one, because of the difficulty of identifying partially digested trout, unidentifiable fish would simply be excluded

from the tally. Recent re-analysis of the diet data (Matuszek et al. 1990) reveals a much higher incidence of juvenile salmonids in the trout stomachs (0.0036) during the period 1936-1949 than noted by Martin (1970), suggesting that Martin excluded from his tally of cannibalism any records that were not positively identified as lake trout. If the reported salmonids in the stomachs during 1936-1949 were lake trout juveniles, and this seems likely as the only other salmonid in the lake is the brook trout (*Salvelinus fontinalis*) which is rare, the total number of juveniles eaten during the survey in those years would be 4530 ($0.0036/0.0040 \times 5033$). Expansion of this estimate to the entire year gives a total annual consumption of 10,872 juvenile trout. Based on our population model (p. 107), the estimated number of juvenile lake trout extant in any given year, at present is about 37,000, indicating a possible annual mortality due to cannibalism of about 8.8-29.4%. The estimated annual mortality of juveniles age 1 to 3 yr, for the present Lake Opeongo population, is about 35% (based on our model). Therefore, cannibalism could possibly account for a large component of the annual juvenile mortality.

Lake trout cannibalism has been reported in several studies suggesting that it occurs widely in lake trout populations (Martin and Olver 1980). For example, the occurrence of cannibalism was 0.028 in Great Bear Lake in the Canadian Northwest Territories (Miller and Kennedy 1948; Johnson 1975), 0.079 in Museum Lake, Quebec (Martin 1955), 0.029 in Lake Michigan (Chiotti 1973), and 0.005 in both Twin Lakes, Minnesota (Griest 1977), and Lake Minnewanka, Alberta (Cuerrier and Schultz 1957). At these rates, cannibalism would appear to be a significant cause of mortality among juvenile lake trout and to have the potential for regulation of population size by limiting juvenile survival and recruitment when adults are abundant. There is evidence (Martin and Olver 1980; MacLean et al. 1981) that juvenile hatchery-reared fish experience greater annual mortality than their wild counterparts.

LAKE TROUT POPULATION MODEL: SIMULATING POPULATION RESPONSE TO STRESSORS

An age-structured simulation model was developed to explore the population changes caused by the three most prominent stressors operating on various life stages of lake trout: exploitation, eutrophication and loss of early life habitat, and stocking of non-native lake trout. Factors evaluated include: mortality due to fishing; the effect of variable egg and YOY survival; and the combined

effects of stocking and fishing on the genetic and numerical composition of lake trout populations through time. Our intention is to provide managers with a computer model that is relatively easy to use, and that can be employed to provide guidance in making management decisions concerning exploitation rates and allowable harvests, habitat protection and rehabilitation, and lake trout stocking strategies.

MODEL DESCRIPTION AND RATIONALE

The computer model was developed to simulate the effects of anthropogenic stressors on wild, native lake trout populations. Our objective was to build a computer model that is structurally consistent with our conceptual model of lake trout population dynamics and then to explore how the model responds as parameters are varied in realistic ways. The model, while parameterized using the Lake Opeongo stock-recruit function, is not intended to simply simulate the dynamics of the Lake Opeongo population. Our intention was to provide a model that is generally applicable to inland lakes in Ontario. At present, the model does not allow for a lake area adjustment (see Payne et al. 1990), therefore, the level of recruitment corresponds to a hypothetical lake with area similar to Lake Opeongo. Nevertheless, we expect that the model will simulate the responses to fishing, environmental change and stocking, typical of lake trout populations in general. The usual Ricker stock-recruitment function (Ricker 1975) relating recruits to adult female abundance was transformed to relate survival rates of juvenile trout (ages 1, 2, and 3 yr) to the abundance of all adults age 6 yr and older, in accordance with our cannibalism-recruitment hypothesis. The standing stock of fish aged 1-20 yr in each year is based on the number of fish alive in each age category at the end of the preceding year. Egg production is a simple function of the biomass of female adults aged 6-20 yr.

The model is designed to accommodate natural recruitment of wild trout, stocking of hatchery-reared, yearling lake trout and natural recruitment from hatchery trout. Survival of wild and stocked trout is tabulated separately, but the combined abundance of wild and hatchery-origin adult trout is used to determine the survival rates of the 1, 2, and 3 yr-olds of wild and hatchery origin. Three reproductive scenarios can be accommodated:

- no natural reproduction of wild or domestic trout;
- natural reproduction of wild trout, but no reproduction of hatchery trout; and
- natural reproduction of wild and domestic trout, with survival from egg to age 1 yr being set independently and at any desired level for the wild and hatchery fish.

Natural mortality from egg to age 1, natural mortality of trout age 4 and older, fishing mortality, growth and fecundity were set independent of stock density. The model is deterministic, in that parameters are not subject to stochastic (random) variation. Egg and adult mortality rates were specified at the outset of each simulation. While mortality rates are fixed at predetermined values, the user can easily pre-select for changes in mortalities of eggs and fish ≥ 4 yr at specified years during the simulation. Natural mortality from egg to age 1, natural mortality of adults, and fishing mortality is determined by the user at the outset but, as noted, mortality rates for juveniles ages 1, 2, and 3 yr are determined automatically during each simulation.

Under reproductive scenario 3, natural progeny of hatchery trout (ages 1 and greater) are tabulated with the progeny of wild trout, because they would not normally be distinguishable in the field. At present, there is no information about the extent of interbreeding between wild and domestic lake trout, although some observations suggest that segregation might occur at spawning time (MacLean et al. 1981). In all cases herein, however, we have assumed complete mixing and interbreeding between wild and native progeny. Clipped, first generation hatchery fish, when allowed to reproduce, were restricted to breeding only with fish of hatchery origin.

Survival

The model employs the instantaneous total mortality rate (Z) to determine the number of fish surviving in each age group each year. The standard time interval for all calculations in the model is 1 yr, with the exception of egg to age 1. The number of fish surviving is obtained by

$$N_{i+1, t+1} = N_{i,t} e^{-(F+M)} \quad [1]$$

where e = base of the natural logarithm

Z = instantaneous rate of total mortality = $M + F$

M = instantaneous rate of natural mortality

F = instantaneous rate of fishing mortality; and

$S = N_{i+1, t+1} / N_{i,t}$ = rate of survival

Instantaneous rates of fishing (F) and natural (M) mortality are determined separately for three discrete life stage intervals as follows:

Eggs to age 1 - Fishing mortality (F) is assumed to be 0 for this life stage. Natural mortality for eggs to age 1 yr (M_0) is supplied by the model user. Two different values can be used simultaneously for eggs of native versus stocked fish.

Age 1-3 - Fishing mortality (F) is also assumed to be 0 for ages 1-3 yr. Natural mortality for ages 1-3 yr (M_1) is determined by the model as a function of the biomass of lake trout age 6-20 yr. The recruitment function is based on a Ricker (1975) stock-recruitment function for the Lake Opeongo lake trout population of the form:

$$R = \alpha P e^{-BP} \quad [2]$$

where R = number of recruits at age 1

P = biomass of mature females

α = a fitted coefficient = 7.31

B = a fitted coefficient = 0.00042

The Ricker function (B.J. Shuter, OMNR, pers. comm., unpubl. data.) was transformed so that survival from age 1 to 3 was dependent on the biomass of all adult fish of age ≥ 6 yr as follows:

$$S_{1-3} = a e^{-BP_A} \quad [3]$$

where S_{1-3} = survival age 1-3 yr

a = 0.900

B = 0.00016

P_A = total biomass of fish age ≥ 6 yr

Transformation of the new function using natural logarithms yields:

$$M_1 = \frac{[(-0.00016 P_A) - 0.10536]}{3} \quad [4]$$

where M_1 = the instantaneous natural mortality rate for ages 1, 2, and 3 yr.

The rationale for this transformation of the stock-recruitment relationship is described above in our cannibalism-recruitment hypothesis.

Natural mortality of the juveniles is not allowed to fall below 0.10, even though lower values will be determined by the recruitment function. This prohibits annual survival of juvenile fish from exceeding 90%. We assume that at low densities of adult trout, other mortality factors, such as predation or competition by other species, would check survival rates. Survival of first generation hatchery juveniles can be set as any fraction of the survival of wild juveniles from zero (no survival) to 1.0 (the same survival rate as the wild juveniles).

Age 4 and older - The user must supply the instantaneous rate of fishing mortality (F) for fully recruited lake trout. The model assumes this applies to fish 8 yr and older and applies a proportion of this value to younger fish (proportions are based on vulnerability for Lake Opeongo lake trout, B.J. Shuter, OMNR, pers. comm.). More recent values for fishing vulnerability of Lake Opeongo lake trout are provided by Payne et al. (1990) as follows:

Instantaneous rate of fishing mortality	
<u>Age</u>	<u>Model</u>
4	.12 * F
5	.30 * F
6	.57 * F
7	.75 * F
8 and older	F

Natural mortality of the older juveniles and adults (M_2) is constant for all fish aged 4 and over, and is supplied by the user. In all simulations, natural mortality was set at 0.10 for all fish ≥ 4 yr.

Growth and Egg Production

Growth is not a density-dependent variable in this model. However, weight must be determined for each age group, in each year of the model, in order to derive total biomass values of fish 6 and older and egg production values.

The von Bertalanffy equation was used to determine fork length (FL) (cm), for a typical Ontario lake trout populations, as follows:

$$FL = 59.9 (1 - e^{-0.168 (t-0.189)}) \quad (\text{Payne et al. 1990}) \quad [5]$$

Fork length was then converted to weight according to the relationship provided by Martin and Olver

(1980) for Lake Opeongo lake trout from 1953-1965:

$$\text{Log}_{10} (\text{weight}) = -2.17984 + 3.09839 \text{ Log}_{10} (FL) \quad [6]$$

A constant of 1.6 eggs g⁻¹ (Martin and Olver 1980) of adult female lake trout (age 6 and older) was used to determine total annual egg production. It is assumed that all adult females (≥ 6 yr) spawn every year and that the sex ratio of adult fish is 1:1. Mortality from egg to age 1 yr accounted for all losses from body cavity egg to the yearling stage.

Model Simulations

Several input parameters must be specified prior to each run of the model as follows:

- The number of years that the model is to run;
- The initial population structure must be specified by providing the number of fish in each age group from 1 to 20 yr. The maximum age has been arbitrarily set at 20 yr;
- The instantaneous mortality rate for egg to 1 yr, and the instantaneous natural and fishing mortality of adults are required as well as any changes in these values and the years at which changes are to be introduced during the simulation;
- If hatchery fish are to be stocked, the year and number of fish to be stocked must be specified. Each change to the stocking schedule must be specified at the outset;
- If hatchery fish are stocked, the reproductive status must be specified. If natural reproduction of the domestic fish does occur, the mortality rate for the egg to yearling stage must be specified independently of the progeny of native fish; and
- If stocking occurs the survival rate of the stocked trout (ages 1, 2, and 3) must be specified as a fraction of the survival of the wild juveniles. Survival of the wild juveniles varies during each simulation as a function of the biomass of adult trout.

The model was tested for its ability to simulate the approximate equilibrium structure of the present Lake Opeongo population. The ability of the model to simulate the "observed" structure of the population based on virtual population estimates (Fig. 51, Panels B and C) and to attain stability over 100 yr at the presently observed levels of natural and fishing mortalities of the adult trout was taken as evidence that the model was performing satisfactorily. Further evidence of the general

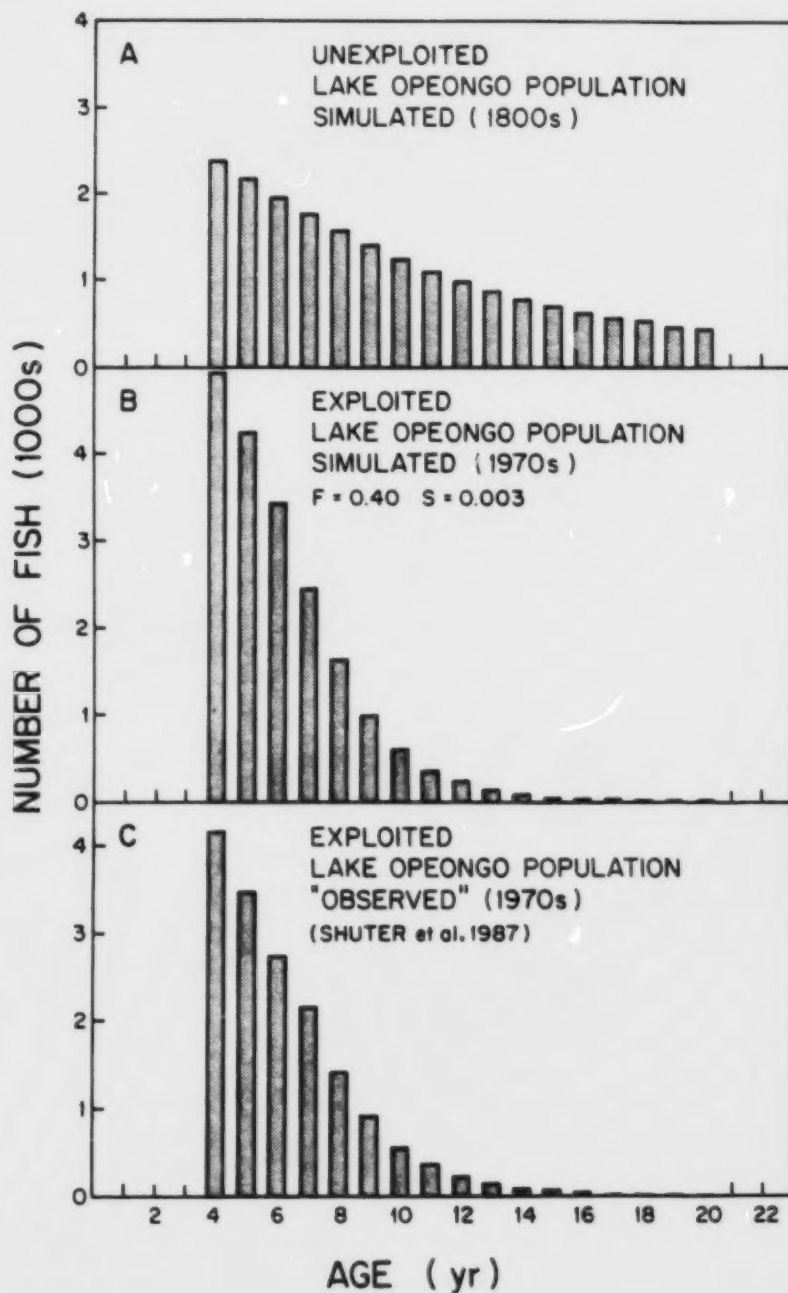


FIG. 51. Comparison of the "observed" (virtual population estimate) lake trout population structure in Lake Opeongo during the 1970s, with the simulated population structure for the 1970s and the unfished population during the 1800s using our computer model.

robustness of the model was its ability to attain equilibrium when fishing mortality was removed. The predicted equilibrium structure of the unexploited population (Fig. 51, Panel A) is similar to that expected based on existing population theory for lake trout (Power 1978).

EFFECTS OF VARYING INTENSITY OF EXPLOITATION

We used the simulation model to explore the effects of variation in exploitation rate at a constant level of egg and YOY survival. The level of early survival chosen was the approximate mean survival from body-cavity egg to age 1 (i.e. 0.003) for the Lake Opeongo lake trout as determined by "backcasting" from the known adult age structure using the simulation model. We have addressed four specific questions as follows: (1) how does exploitation influence the number and biomass of lake trout age 6 yr and older?; (2) how does exploitation affect the number of recruits into the fishery at age 4?; (3) how does exploitation affect the mean weight of adult trout in the population?; and (4) how does exploitation affect the age structure of the population of trout age 4 yr and older?

Simulations were run for 100 yr at various fixed rates of instantaneous fishing mortality from zero to $F = 1.6$. For each of the following: number and biomass of adults, the number of 4 yr-old recruits and the age structure of the population, we averaged the annual estimates for years 76 through 100 to provide a description of the response of the population at each selected level of exploitation. Survival from egg to yearling was fixed at 0.003 and natural mortality at $M_2 = 0.1$ for all simulations.

The number of adult lake trout in the population declines almost linearly as exploitation increases from zero to $F = 1.6$, and M is fixed at 0.1 (Fig. 52a). The biomass of trout declines in an exponential trajectory, with a 50% reduction in biomass occurring at an instantaneous fishing mortality (F) of 0.4 and a total mortality of about 40% per year ($Z = 0.4 + 0.1$; $A = 0.4$) (Fig. 52b). At $F = 0.7$ and $Z = 0.8$ (total annual mortality (A) of 55%), the biomass declined by more than 80% of the unexploited level (Fig. 52b). This level of total annual mortality (i.e. $Z = 0.8$) is representative of the approximate median level of mortality in exploited lake trout populations in Ontario, based on scale age assessment (Fig. 53). Mortality rates might be seriously overestimated, however, because of the tendency of scale ages to underestimate the true age (e.g. Power 1978).

At the selected level of egg to yearling mortality (0.003) our simulated population has a maximum capacity to compensate for exploitation over the range $F = 0.2-0.6$, as indicated by the number of

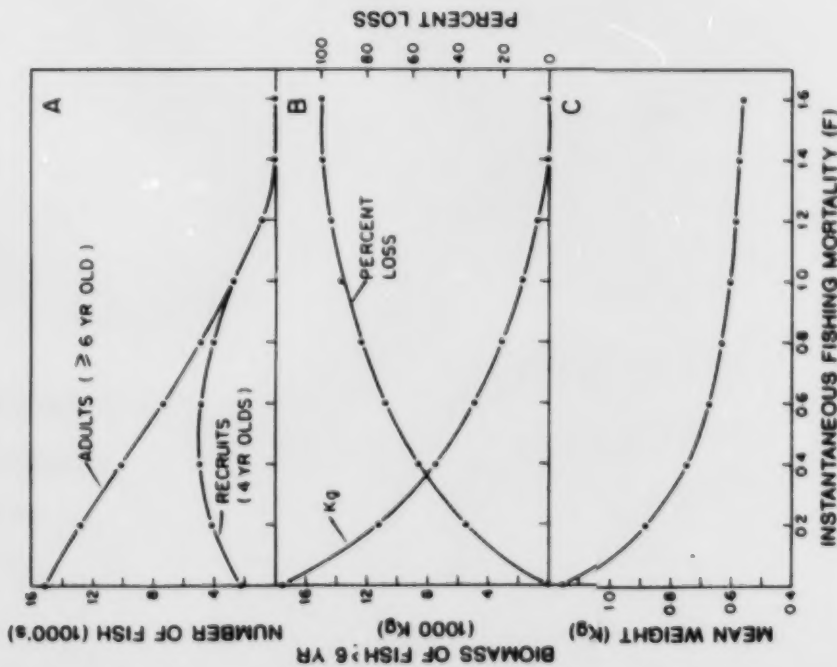


FIG 52. Simulated number of 4 yr-old recruits and number, biomass, and mean weight (kg) of adult lake trout in a hypothetical 6000 ha lake under various instantaneous fishing mortality rates. The annual survival rate from egg to yearling stage was fixed at 0.003 and the instantaneous natural mortality of adults was set at 0.1. The percent loss of biomass is expressed as a fraction of the unexploited biomass. Each datum represents the mean value from year 76 to 100 of a 100 yr simulation.

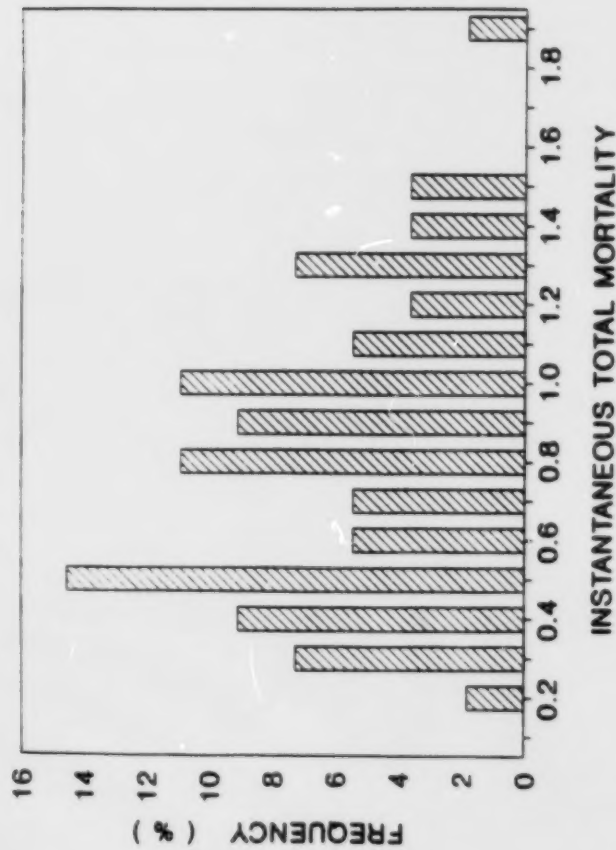


FIG. 53. Frequency distribution of instantaneous total mortality of lake trout populations in Ontario lakes, as determined from catch curves reported in the Lake Trout Summary Data Base. Age assessment was based on scale age evaluations in the majority of cases.

4 yr-old recruits entering the population (Fig. 52a). The number of recruits declines once F reaches 0.8. The mean body weight of adult fish declines rapidly from $F = \text{zero}$ to 0.6, but declines very slowly at higher levels of fishing (Fig. 52c).

Dramatic changes occur in the age structure of a lake trout population over the range of fishing mortality normally observed in Ontario lakes (Fig. 54). At an F of 0.2, fish up to 20 yr of age persist in the simulated population, but at $F = 0.6$, the maximum age drops to 18 yr and the number of adults (≥ 6 yr) is reduced by about 50%. At $F = 1.0$, the maximum age is only 11 yr and the number of adults is reduced a further 50%. The effect of increased fishing mortality, therefore, is especially great on the number of mature adults (Fig. 54).

EFFECTS OF VARIATION IN EARLY SURVIVAL

Under natural conditions, early survival would be expected to vary stochastically, due to the influence of random environmental variation. However, for simplicity, we have set early survival at various fixed levels. Our purpose is to explore the potential effects of factors that might influence early survival. For example, physical reduction in spawning habitat, loss of spawning habitat quality, and reduction in the quantity and or quality of nursery habitat are factors that could potentially reduce early survival. Simulations have been run for an order of magnitude variation in early survival ($\text{egg}^{-1} \text{yr}$) from 0.0005 to 0.005. Each of the selected early life survival rates was tested over a range of instantaneous fishing mortalities from zero to very high rates.

Under each set of early survival and fishing mortality conditions, we have compiled the number of 1 yr-olds, 4 yr-olds, the total population size (age 1-20 yr), and the number and weight of adult trout age 6 yr and older. Each simulation was run for 100 yr, to ensure that the population had stabilized, and the number of fish in each age group (age 1-20 yr) was compiled for each year. The result under each set of mortality conditions was characterized by calculating the average number of fish within each age group for the final 25 years of the simulation (i.e. years 76-100).

The effects of variation in early survival over a range of fishing mortality rates on various components of the population is summarized in Table 28. At each progressively lower level of early survival, the number of adult fish declines steeply, as shown in Fig. 55. This loss of adults is also

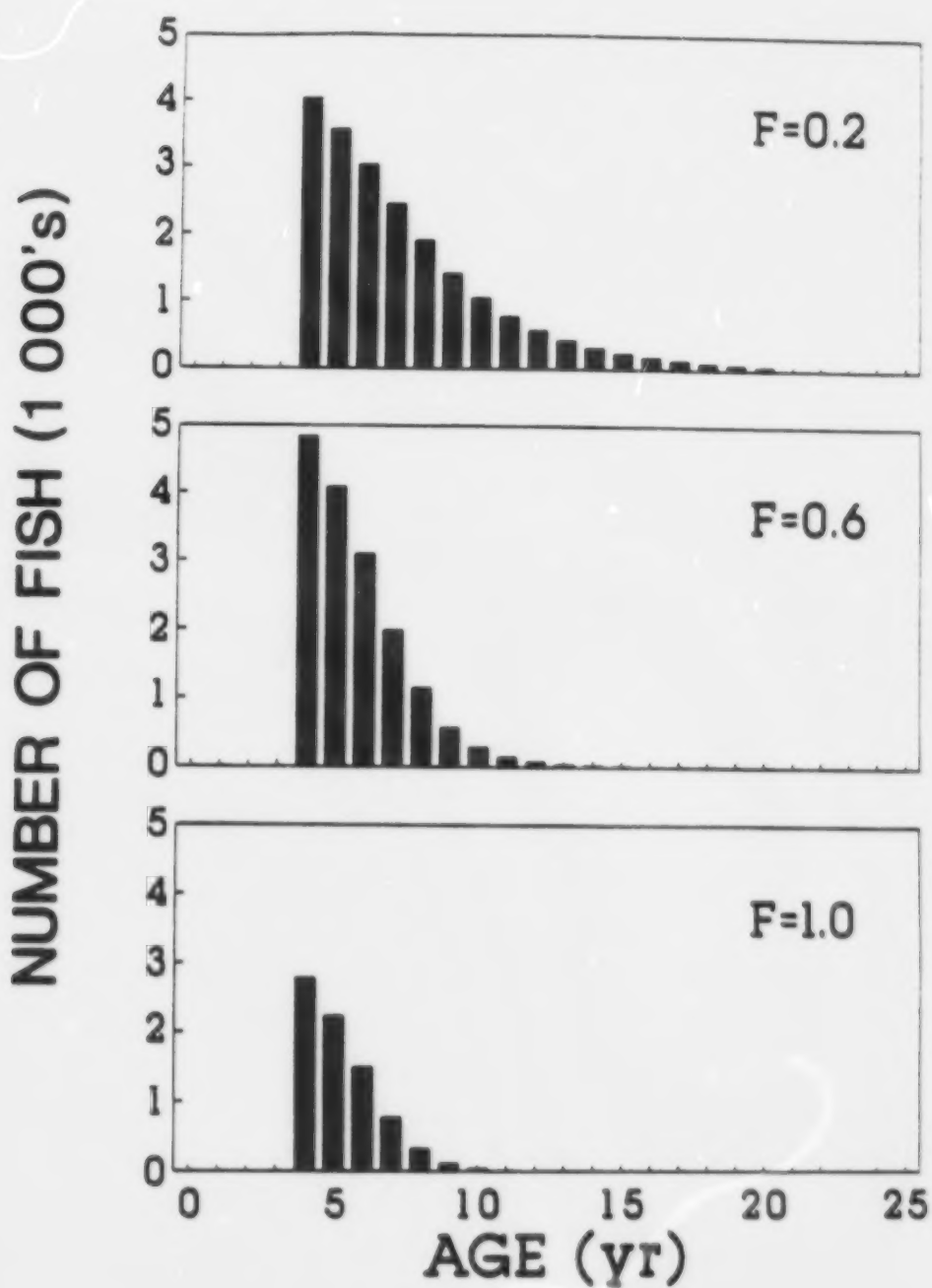


FIG. 54. Population age structures of lake trout age four and older at three rates of instantaneous fishing mortality for a hypothetical 6000 ha lake, as described in Fig. 52.

TABLE 28. Simulated effects of various constant rates of fishing mortality on abundance, biomass and mean weight of lake trout at various fixed survival rates from egg to one year for a hypothetical lake trout population in a 6000 ha lake.

Population component (no. $\pm$ s)	Instantaneous fishing mortality (F)											
	0.0	0.2	0.4	0.6	0.8	1.0	1.2	1.4	1.6	1.8	2.0	2.2
Survival egg yr ⁻¹ = 0.005, mortality rate M ₀ = 5.2983												
1 yr olds	82,757	57,637	43,452	34,694	30,430	23,699	16,540	10,636	6,110	2,009	456	101
s	4,008	240	3,896	11,653	14,047	12,247	8,047	4,412	1,485	396	143	45
# $\geq$ 1 yr	141,055	120,999	106,613	99,093	93,867	80,420	63,244	44,216	26,141	9,058	2,137	492
s	1,748	149	2,850	8,822	11,987	11,477	9,037	5,451	2,143	1,231	588	205
# 4 yr olds	2,771	5,169	6,821	8,977	9,946	9,807	8,894	6,771	4,158	1,529	377	91
s	375	63	1,303	5,132	7,434	7,239	5,600	3,266	1,229	306	121	43
# $\geq$ 6 yrs	17,751	16,291	14,534	13,592	11,694	9,763	7,010	4,933	2,720	859	190	41
s	965	100	1,696	5,168	6,298	5,523	3,754	2,029	675	149	54	17
wt. $\geq$ 6 yrs	20,575	14,413	10,841	9,059	7,414	5,899	4,093	2,795	1,519	473	103	22
s	1,052	61	979	2,992	3,557	3,049	2,051	1,084	362	81	29	9
Mean wt.	1.160	0.885	0.748	0.684	0.662	0.628	0.598	0.574	0.560	0.551	0.543	0.536
s	.043	0.002	0.029	0.071	0.084	0.072	0.051	0.033	0.015	0.007	0.007	0.007
Survival egg yr ⁻¹ = 0.004, mortality rate M ₀ = 5.5215												
# 1 yr olds	61,729	41,545	29,689	21,689	16,187	11,300	7,007	3,477	800	156		
s	2,021	60	732	2,451	2,074	2,198	1,268	381	180	59		
# $\geq$ 1 yr	112,020	44,651	80,855	68,475	57,165	44,111	30,342	15,909	3,749	752		
s	1,420	140	599	1,986	2,976	2,557	1,537	726	736	261		
# 4 yr olds	2,561	4,652	6,021	6,655	6,654	5,890	4,599	2,574	628	131		
s	214	7	247	1,273	1,892	1,564	1,019	288	131	47		
# $\geq$ 6 yrs	16,652	14,665	12,390	10,205	7,974	5,780	3,796	1,904	419	79		
s	563	21	397	1,256	1,673	1,246	688	213	85	27		
wt. $\geq$ 6 yr	19,256	12,978	9,237	6,851	5,035	3,491	2,213	1,084	234	43		
s	649	18	231	721	940	685	376	116	48	15		
Mean wt.	1.157	0.885	0.746	0.673	0.635	0.607	0.584	0.570	0.560	0.551		
$\geq$ 6 yrs	0.006	0.000	0.002	0.004	0.006	0.005	0.003	0.001	0.001	0.001		

TABLE 28. Continued

Population component (no. $\pm$ s)	Instantaneous fishing mortality (F)											
	0.0	0.2	0.4	0.6	0.8	1.0	1.2	1.4	1.6	1.8	2.0	2.2
Survival egg yr ⁻¹ = 0.003, mortality rate M ₀ = 5.8091												
# 1 yr olds	42,070	26,913	17,897	11,814	7,422	3,985	1,108	176	29			
s	934	107	51	251	283	175	154	57	15			
# $\geq$ 1 yr	83,671	69,028	56,267	43,323	30,788	18,411	5,391	876	147			
s	641	86	156	246	302	342	719	269	74			
# 4 yr olds	2,306	4,023	4,917	4,834	4,073	2,779	867	146	25			
s	122	50	24	148	218	172	116	44	13			
# $\geq$ 6 yr	15,166	12,681	10,015	7,336	4,891	2,743	763	117	18			
s	314	78	35	158	195	137	110	37	9			
wt. $\geq$ 6 yr	17,526	11,217	7,460	4,934	3,086	1,655	763	67	10			
s	390	47	23	0	109	76	110	22	5			
Mean wt.	1.156	0.885	0.745	0.673	0.631	0.603	0.586	0.572	0.560			
s	0.018	0.002	0.001	0.004	0.005	0.005	0.003	0.004	0.008			
Survival egg yr ⁻¹ = 0.002, mortality rate M ₀ = 6.2146												
# 1 yr olds	24,022	13,830	7,827	3,873	1,118	114	13	1.5				
s	314	37	57	38	107	36	7	0.9				
# $\geq$ 1 yr	55,680	42,934	30,506	17,919	5,737	608	13	9.8				
s	236	84	66	58	551	191	7	5.5				
# 4 yr olds	1,961	3,099	3,211	2,370	862	96	12	1.9				
s	55	24	51	41	83	30	6	1.3				
# $\geq$ 6 yr	12,986	9,764	6,561	3,600	1,074	107	12	1.4				
s	145	36	64	40	102	34	7	0.8				
wt. $\geq$ 6 yr	15,016	8,642	4,888	2,422	681	65	7	0.7				
s	195	24	37	23	64	21	4	0.4				
Mean wt.	1.156	0.885	0.745	0.673	0.634	0.608	0.573	0.502				
s	0.010	0.001	0.002	0.002	0.001	0.004	0.025	0.024				

TABLE 28. Continued

Population component (no. $\pm$ s)	Instantaneous fishing mortality (F)											
	0.0	0.2	0.4	0.6	0.8	1.0	1.2	1.4	1.6	1.8	2.0	2.2
Survival egg yr ⁻¹ = 0.001, mortality rate M_0 = 6.9077												
# 1 yr olds	8,581	3,463	688	16	1							
s	30	12	56	9	0							
# ≥ 1 yr	27,691	15,941	3,996	98	7							
s	49	39	326	53	1							
# 4 yr olds	1,384	1,549	526	14	1							
s	12	13	43	8	.5							
# ≥ 6 yr	9,257	4,886	1,119	25	2							
s	31	21	92	14	0							
wt. ≥ 6 yr	10,723	4,326	840	17	1							
s	39	14	69	10	0							
Mean wt.	1.158	0.885	0.751	0.651	0.570							
s	0.003	0.001	0.001	0.018	0.000							
Survival egg yr ⁻¹ = 0.0005, mortality rate M_0 = 7.6009												
# 1 yr olds	2,551	260	11	1								
s	8	33	0.2	0								
# ≥ 1 yr	12,586	1,798	72	8								
s	5	46	0.4	0								
# 4 yr olds	827	202	8.2	1								
s	10	26	0.4	0								
# ≥ 6 yr	5,504	694	26	3								
s	20	89	0.6	0								
wt. ≥ 6 yr	6,376	627	27	2								
s	20	80	0.3	0								
Mean wt.	1.159	0.903	1.041	0.647								
s	0.003	0.002	0.010	0.000								

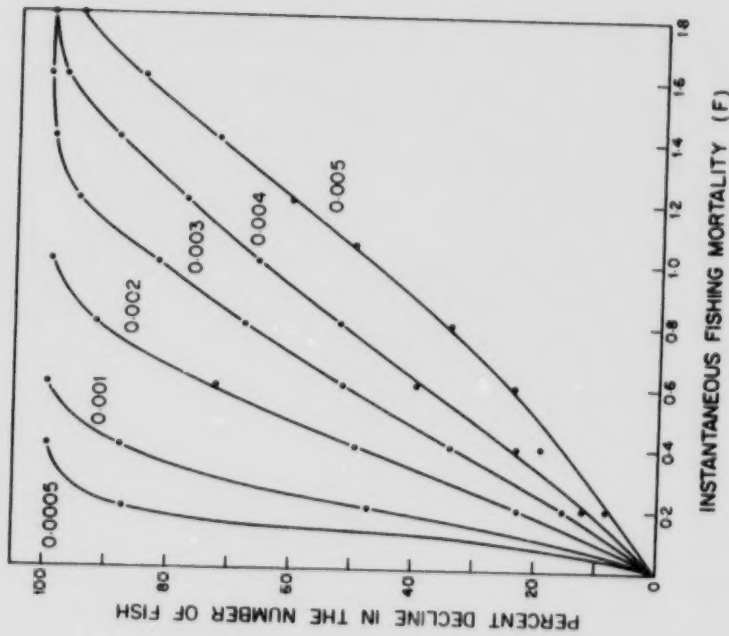


FIG 56. Percent decline in adult population size (fish 6 yr and older) under various combinations of fishing intensity and early survival (body cavity egg to yearling). Percent decline is based on the number of adult trout in the absence of fishing at each rate of early survival.

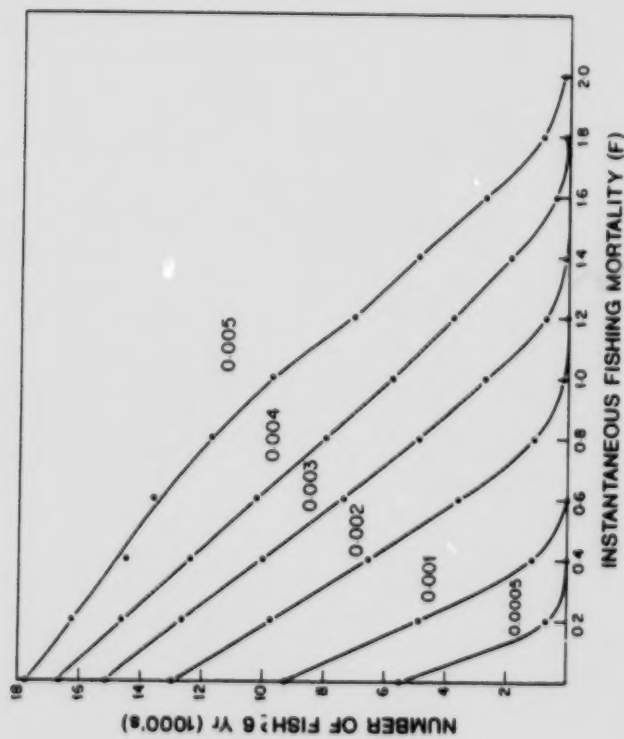


FIG. 55. Relationships between adult population size of a lake trout population in a hypothetical 6000 ha lake under various combinations of fishing intensities and early survival (body cavity egg to yearling).

shown as the percent decline in abundance, relative to abundance at zero fishing mortality, for each level of early survival (Fig. 56). The combinations of early survival and fishing and total mortality that result in 10, 25, 50, 75, and 90% declines in the abundance of adult lake trout (6-20 yr) are summarized in Table 29. According to the model, a population with high early survival (say 0.004) can maintain itself at 50% of the unexploited density at a total annual mortality of 58%. If early survival is reduced by 75% to 0.001, 50% of the unexploited density occurs at a total annual mortality rate of only 27% (Table 29). These simulations illustrate the potentially dramatic effect that reductions in early survival can have on lake trout populations.

Interaction between early survival and fishing mortality has a major effect on the density dependent compensatory capacity of the population, as indicated by the number of 4 yr-old recruits (Fig. 57). When survival rates of the early life stages are high, the compensatory capacity is also high. As early survival is reduced, however, the level of fishing mortality (F) at which the compensatory capacity of the population is exceeded (i.e. the level at which new recruits begin to decline despite

TABLE 29. Instantaneous total (Z) and fishing mortality (F) rates causing 10, 25, 50, 75, and 90% declines in the number of adult lake trout age ≥ 6 yrs at various survival rates from the egg to yearling stage. Survival is calculated from the unfertilized body cavity egg stage, represented by total population fecundity, to age 1 yr. Percent declines were determined from the simulated population structures for years 75-100 of a 100 yr simulation. Percentages are the fraction of the population when fishing mortality is zero at each level of egg survival. Simulations are based on a hypothetical lake trout population in a 6000 ha lake.

Percent decline	Statistic	Survival rate egg yr ⁻¹					
		0.0005	0.001	0.002	0.003	0.004	0.005
10	F	0.04	0.06	0.10	0.13	0.18	0.27
	Z	0.14	0.16	0.20	0.23	0.28	0.37
25	F	0.08	0.13	0.22	0.31	0.41	0.61
	Z	0.18	0.23	0.32	0.41	0.51	0.71
50	F	0.14	0.21	0.41	0.58	0.77	1.05
	Z	0.24	0.31	0.51	0.68	0.87	1.15
75	F	0.16	0.31	0.61	0.89	1.15	1.43
	Z	0.26	0.41	0.71	0.99	1.25	1.53
90	F	0.22	0.42	0.76	1.21	1.42	1.68
	Z	0.32	0.52	0.86	1.31	1.52	1.78

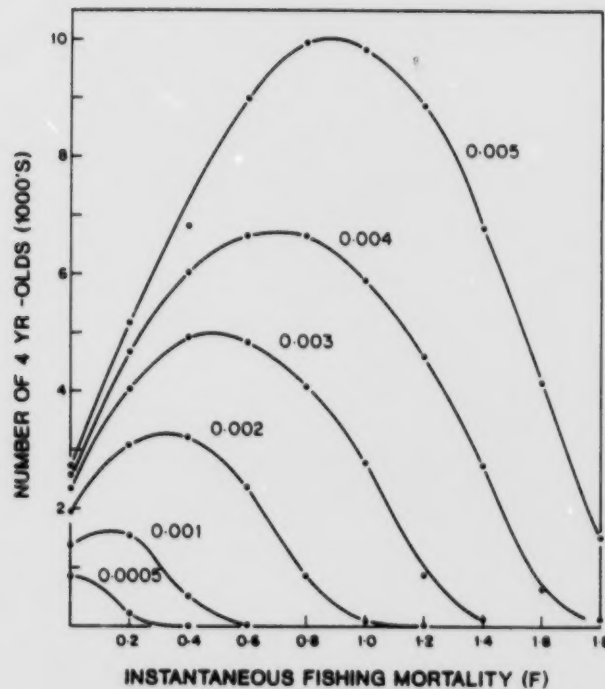


FIG. 57. The number of 4 yr-old recruits entering a hypothetical lake trout population in a 6000 ha lake under various combinations of fishing intensities and early survival rates.

continued reduction in the number of adults) declines sharply from 1.0 at an annual early survival of 0.005 to near zero at 0.0005 (Fig. 57). Over the range of early survival (egg to yearling stage) that appears to be typical of Lake Opeongo lake trout (i.e. 0.002-0.003), density-dependent recruitment compensation is exceeded when F reaches 0.4-0.6 (Fig. 57).

Recruitment overfishing, therefore, will occur over a range of total mortality rates depending on the reproductive capacity (production) of a given stock. Lester et al. (1991) showed that MSY for four lake trout stocks (Bone, Chiblow, Christman, and Flack) occurred at a total annual mortality of 0.50, but that the Opeongo stock was at MSY at a total annual mortality of about 0.35. All of these populations inhabit high quality habitats, suggesting that MSY for many stocks would occur at total annual mortalities much less than 0.5. Figure 57 suggests that early survival in Bone, Chiblow, Christman, and Flack would be approximately equivalent to 0.004 in our model (corresponding to $F = 0.6$ and $M = 0.1$, i.e. $Z = 0.7$ and $A = 0.5$). Similarly, the Lake Opeongo population, with a total

annual mortality of about 0.35, would correspond to an early survival of about 0.002-0.003 ($F = 0.33$; $M = 0.1$; $Z = 0.43$; $S = 0.65$) in our model. Other populations would probably reach MSY at much lower rates of fishing and some could not sustain fishing at all (Fig. 57). Comparison of HUE of lake trout lakes with HUE of the five lakes listed above (Lester et al. 1991), therefore, will only provide a useful indication of fishing exploitation status for lakes having comparable carrying capacities. Less productive lakes would have lower HUE at very low effort, even when they are not overexploited, and their MSY would occur at a much lower effort than for the five reference lakes. Figure 15 suggests how HUE would shift down towards the origin as carrying capacity declines and correspondingly how the critical fishing intensity at MSY would also decline (see Lester et al. 1991, p. 24).

Reduction of 30% in early survival from 0.003 to 0.002, therefore, could very significantly reduce the capacity of our hypothetical population to withstand the stress of fishing. This example reveals the potentially dramatic additive effects of multiple stressors operating simultaneously on a lake trout population. As discussed by Evans et al. (1991), there are numerous anthropogenic factors that can reduce the survival of the early life stages of lake trout in Ontario lakes and which, when coupled with high exploitation rates, would be expected to have dramatic effects on the viability of these populations.

EFFECTS OF STOCKING OF HATCHERY-REARED LAKE TROUT

There are three major ways in which stocking of hatchery-reared lake trout may have a detrimental effect upon native populations of lake trout. These are: (1) altering the genetic constitution of the native fish; (2) displacing native fish from spawning sites; and (3) by causing increased exploitation rates on native fish.

Introgressive Hybridization

Supplemental stocking of hatchery-reared lake trout may cause substantial detrimental genetic impacts on native populations. This concern is based on the premise that native fish stocks are better adapted to their local habitats than non-native stocks, and that introgressive hybridization between native and introduced fish is a common occurrence. Introgressive hybridization is the invasion of

genes of one species or stock into the gene pool of another. A considerable body of evidence has been produced to support these hypotheses (Altukhov 1981; MacLean and Evans 1981; Ryman and Stahl 1981). Furthermore, it has been argued that the larger the difference in environmental history of the native and donor stocks, the larger the potential genetic impact. In this regard, hatchery stocks are of particular concern because they are often genetically very different from wild stocks, due to hatchery rearing and breeding practises. Not only can hatchery stocks become adapted to very artificial environmental conditions, but they can also suffer a substantial reduction in genetic variability compared to wild stocks. Genetic changes and loss of genetic variability in hatchery stocks have been reported repeatedly (e.g. Allendorf and Ryman 1986 and refs. therein). The loss in fitness, associated with reduction in genetic variability due to inbreeding, has been well documented in a variety of animal species, including fishes (Allendorf and Leary 1986).

Adaptation to local conditions of native stocks has been demonstrated for a number of species of fish, including lake trout. Plosila (1977) showed that transplanted stocks of lake trout had lower fitness, in terms of survival, than stocks planted into their native habitats. Natural reproduction from transplanted hatchery-reared lake trout has been shown to be much lower than that from native stocks (Krueger et al. 1986). Ihssen et al. (1988) have shown that transplanted stocks of lake trout have less genetic variability than the donor stocks from which they originated. Altukhov and Salmenkova (1988) reported that transplanted chum salmon (*Oncorhynchus keta*) returned to spawn at the rate of only 0.03%, compared to 0.4% to 0.7% for native chum salmon. In general, transplanted salmon have given much poorer returns than native salmon (Okazaki 1978, 1982; Withler 1982). Altukhov and Salmenkova (1988) claim an inverse relationship between rate of return and the genetic distance between donor and recipient stocks.

Non-native donor stocks used for supplemental planting can have a genetic impact on native stocks via introgression. The stock or species of higher fitness or abundance tends to replace the other stock or species. No example of this phenomenon has been documented for lake trout (but see circumstantial evidence in Ihssen et al. 1988). However, both intraspecific and interspecific introgression in fishes is a common occurrence. The method of electrophoresis has made it possible to trace the introgression of non-native genes into local gene pools. For example, extensive transplanting of rainbow trout (*Oncorhynchus mykiss*) has led to introgressive hybridization with several indigenous stocks and species (Allendorf et al. 1980; Busack and Gall 1981; Campton and

Johnston 1985) and, in some cases, the elimination of the native species (Allendorf and Phelps 1981). Introgression has also been reported for brown trout (*Salmo trutta*) (Ryman 1981), bass (Whitmore 1983) and minnows (Hubbs 1955). Since introgression occurs readily, even between species, it is expected that it is also a likely occurrence between planted and native lake trout stocks. Within species introgression probably occurs more often than interspecific introgression, but has not been reported as frequently because it is less readily observed. Genetic techniques, such as enzyme electrophoresis and recombinant DNA procedures, are needed to detect intraspecific introgression, whereas interspecific introgression can usually be deduced from morphological characters.

It has been suggested that a small amount of introgression of closely related stocks can be beneficial (Allendorf 1983). In general, however, introgression has detrimental effects that range from the complete elimination of a species to more subtle genetic effects that can be detected only a number of generations after the initial genetic contact. It is thought that introgression causes the break-up of adaptive gene complexes, in addition to loss of genetic variability, if the introduced stock has reduced genetic variability. It may seem paradoxical that a less fit donor stock can replace the better adapted local stock. The mechanism that has been proposed is that an environmental disturbance can initially provide conditions that favour introgression. Due to an anthropogenic impact, the environment may even temporarily favour the non-native stock. The first generation hybrid (F_1) can have a fitness advantage of hybrid vigor, and out-compete the native stock. In subsequent generations, as the local and introduced genes segregate and hybrid vigor declines, a less fit stock results. Continuous planting can eventually completely replace the native gene pool with the donor gene pool. The donor stock does not need to be as well adapted to local conditions, because it goes through part of its life cycle under much less demanding conditions in a protected, constant hatchery environment. This lower fitness of the introduced stock will only become evident after planting is discontinued, and the introduced stock is obligated to pass successfully through that part of the life cycle it previously spent under hatchery conditions.

Segregation of Native and Hatchery-Reared Lake Trout During Spawning

Physical displacement of native lake trout from all or favoured spawning sites could result when large numbers of hatchery fish are stocked. Whether this actually prevents native fish from spawning or causes them to spawn under less favorable circumstances, is not known. In either case, the result would be decreased reproduction. There is some evidence of segregation having occurred between

native and hatchery lake trout in Lake Simcoe, Ontario (MacLean et al. 1981). These authors also found evidence of segregation at spawning time among domestic stocks of different origins.

Interaction Between Stocking and Exploitation

Stocking of hatchery-reared lake trout into a lake inhabited by a self-sustaining population of native lake trout can have a detrimental effect on the native fish by causing and supporting a high rate of exploitation. Hatchery-reared trout stocked as yearlings can sustain high rates of fishing because their recruitment is not dependent on the vagaries of the natural environment during the first year of life when most of the natural mortality would normally occur. Thus, the hatchery fish can be artificially replenished essentially as fast as they are removed by the fishery. When the stocking rate of yearlings (i.e. artificial recruitment) exceeds the natural recruitment rate of wild native trout and both wild and domestic yearling and older fish are subject to losses due to fishing that exceed the natural replacement rate, the domestic trout will, over time, replace the native stock. This process is accelerated when exploitation rates are high because loss of older native trout, which is some probabilistic function of fishing intensity over time, reduces the reproductive capacity and recruitment of the native population. High exploitation rates are of little consequence to the domestic component of the population because their recruitment is not dependent on reproductive success in the lake.

A combination of the effects of stocking, exploitation and introgressive hybridization will quickly lead to the loss of wild stocks. If stocking stimulates fishing pressure, the loss of wild fish will be accelerated thereby reducing their abundance and increasing the probability of interbreeding and introgression with trout of hatchery origin. Our analyses indicated that stocked lake trout populations were more heavily exploited than unstocked populations (Table 18a, b). This effect was particularly insidious in that stocking can maintain high levels of exploitation, giving the erroneous impression of a healthy stock. The genetic make up of the fish is not something that is readily observable, nor are the implications of weakening the gene pool of the population immediately obvious. Given the lower fitness and reduced reproductive viability of transplanted lake trout stocks (Plosila 1977; Krueger et al. 1986), substitution and, or, introgression of native lake trout stocks in Ontario lakes is a major ecological threat to the viability of the species. Our evaluation of the status of the lake trout resource in Ontario shows that only 64% of the populations are comprised of wild native stocks (i.e. have never been stocked), however in Northeastern Region, where 35% of Ontario's lake trout lakes are located, only 54% are unstocked, wild populations.

In the following section, we develop a simulation model to explore the combined effects of stocking and exploitation on the genetic and numerical composition of lake trout populations.

MODELLING INTERACTION EFFECTS OF EXPLOITATION AND STOCKING

We explored the effect of stocking of hatchery-reared yearling lake trout on the adult (6-20 yr) population size and biomass. We also examined the contribution to the population of trout of hatchery origin under various reproductive and juvenile survival scenarios. The model was run for the following scenarios:

- juvenile survival of the stocked trout equal to the wild trout, with normal reproductive success of the wild trout, but no natural reproduction of hatchery trout;
- juvenile survival of the stocked trout equal to that of the wild trout, and reproductive success of the hatchery trout equal to that of the wild trout;
- juvenile survival of the stocked trout one half that of the wild trout, but reproductive success equal to that of the wild trout; and
- juvenile survival of the stocked trout one half that of the wild trout and reproductive success also one half that of the wild fish.

Normal reproductive success was set at an early survival rate of 0.004 from body cavity egg to the yearling stage. This represents very strong early survival characteristics in a pristine environment, therefore, the simulations provide very near ideal conditions for the performance of wild fish in the presence of stocked hatchery-reared lake trout. Survival of the wild juveniles was set as a function of adult biomass as specified by the model.

In the first set of simulations, we assessed the effect of stocking at a fixed rate of five yearling trout ha^{-1} under varying fishing mortality rates, on the number, biomass, and percent loss of mean body weight of adult fish, and the percent hatchery fish in the population. Instantaneous fishing mortality varied from zero to 1.8 and instantaneous natural mortality of post-juveniles was maintained at 0.1. In the second set of simulations, we assessed the effects of varying the stocking rate at a fixed level of instantaneous fishing mortality. Stocking rates employed were 1, 3, and 5 yearlings ha^{-1} and instantaneous fishing mortality (F) was set at 0.8.

Effect of Variable Fishing Mortality at a Fixed Stocking Rate

The first set of simulations revealed that stocking of hatchery-reared fish can have several important effects on a native fish population. If we use the population curve for a wild self-sustaining population as a reference base, it appears that stocking of hatchery-reared trout can increase the abundance of adults over all levels of fishing intensity (Fig. 58). It is also apparent that the effect of stocking is dependent on the level of exploitation, hatchery fish making the greatest contribution when fishing mortality is very high ($F > 0.6$). Increase in population size with stocking is also strongly dependent on the viability of the hatchery fish with regard to their post-stocking survival and reproductive ability.

The greatest contribution of hatchery trout to the quantity of fish occurs when the survival of the hatchery and wild juveniles is equal (Fig. 58, curve A). For present purposes, we assume that the survival of hatchery juveniles never exceeds that of the wild juveniles. The contribution of the hatchery fish is very substantially reduced if they are unable to reproduce (Fig. 58, curve B). The contribution is reduced even further, however, if the survival rate of the hatchery juveniles is reduced by one half that of the wild juveniles (Fig. 58, curve C). Indeed, the difference between curve C and the wild trout baseline in the absence of stocking (curve D) is only about 8% at $F = 0.4$, 25% at $F = 0.8$, and 60% at $F = 1.2$ (Fig. 58). The parallel effects of stocking on the adult biomass, including the percent decline in mean body weight, are shown in Fig. 59.

Stocking has a dramatic effect on the genetic composition of a lake trout population (quality of fish) as revealed by Fig. 58, curves B, D, and E. An increase in the total abundance of lake trout occurs when there is no reproduction by the hatchery trout (curve B), but the number of wild fish contributing to the population in this situation is dramatically reduced as shown by curve E. The presence of large numbers of hatchery fish in the population causes reduced survival of wild juveniles (curve E at $F = 0$) and this effect is simply magnified as fishing pressure intensifies. The combination of stocking and fishing causes a transformation of the population from one consisting entirely of wild fish to one dominated by trout of hatchery origin. The implications are especially serious, if the hatchery fish are not from the same stock as the wild population. Stocking of non-native lake trout stocks is a common practise in Ontario lakes (Evans et al. 1991). Extensive stocking of one genetic stock of hatchery fish would cause the genetically diverse wild stocks to be replaced by a genetically less variable domestic stock, thereby weakening the stock and species through the loss of natural genetic variability (see Ihssen et al. 1988).

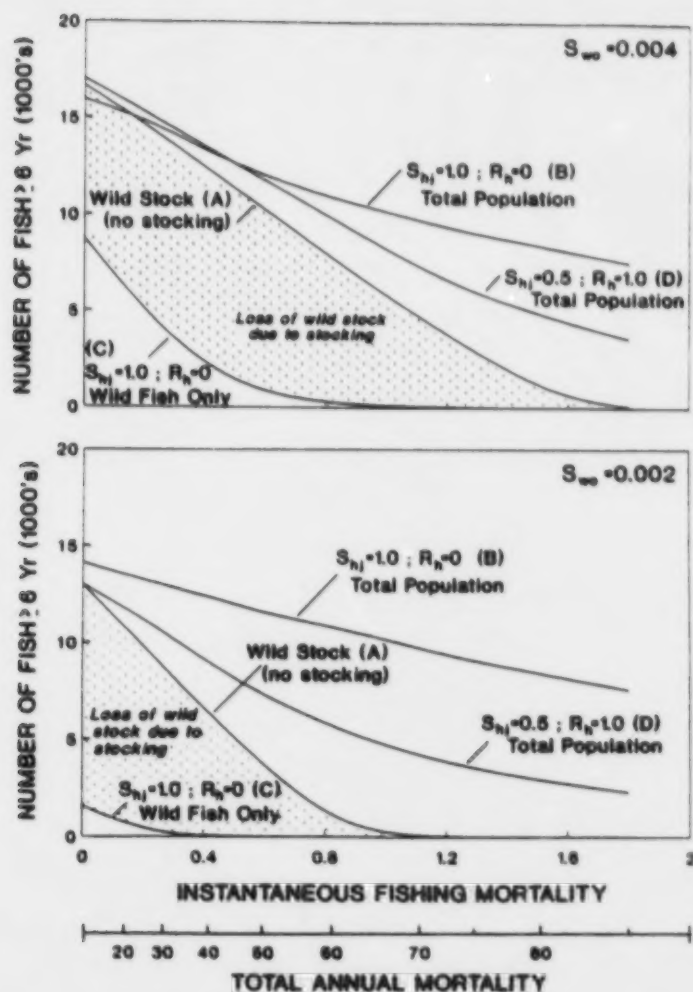


FIG. 58. The number of adult lake trout in a hypothetical population in a 6000 ha lake under various levels of fishing mortality in the absence (curve A) and presence (curves B, C, and D) of stocked yearling lake trout, when eggs to yearling survival is high ($S_w = 0.004$, upper panel) or low ($S_w = 0.002$, lower panel). Stocking scenarios include the annual release of 30,000 yearlings (5 ha^{-1}) in each case. Two levels of survival of the first-generation hatchery juveniles (ages 1, 2, and 3 yr) were used with survival either equal to the wild juveniles ($S_{H1} = 1.0$) or to one half that of the wild juveniles ($S_{H1} = 0.5$). Two reproductive scenarios were also used, either no reproduction of hatchery trout ($R_H = 0$) or reproduction of hatchery trout equal to that of the wild trout ($R_H = 1.0$). The shaded area represents the loss of wild trout due to the combined effects of exploitation and stocking. The simulations of 100 yr were run at each level of egg to yearling survival.

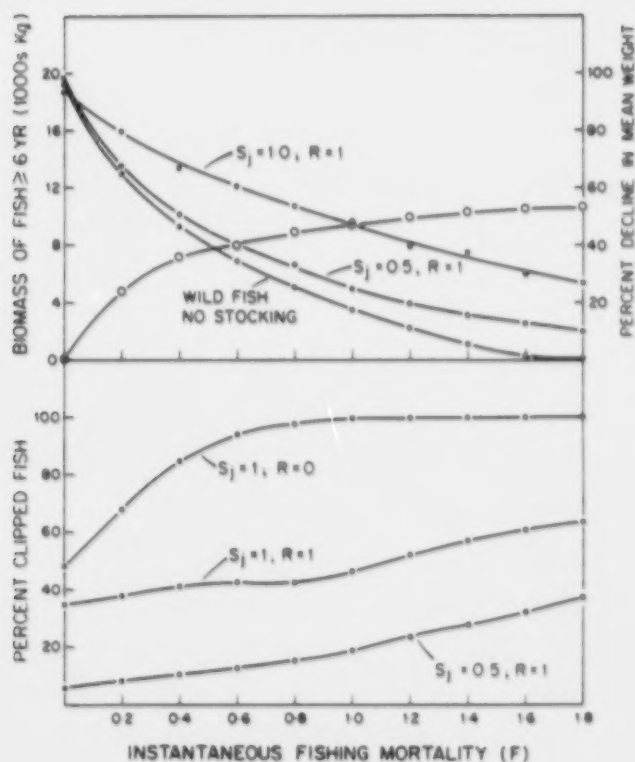


FIG. 59. The biomass, decline in mean body weight, and the percent clipped (first generation hatchery) lake trout in a hypothetical population in a 6000 ha lake under various fishing intensities, at an annual rate of early survival of 0.004 in the presence and absence of stocking of hatchery-reared yearling lake trout. Symbols and conditions are as described in Fig. 58

High early survival - The effect of annual stocking at a fixed rate on a self-sustaining lake trout population having strong early survival ($S_{\text{we}} = 0.004$) is shown in Fig. 58 (upper panel), for two reproductive scenarios. Simulations were run at fishing mortalities from $F = 0$ to $F = 1.8$, at increments of $F = 0.2$. Each simulation was run for 100 yr and a mean population for years 76 to 100 was calculated to obtain the population structure representative of the obtaining conditions (Table 1). Figure 58, curve A, indicates the predicted decline in adult population size as fishing mortality increases in the absence of stocking. When five yearling lake trout were stocked ha^{-1} and their survival as juveniles (S_j) was identical to the wild juveniles, and the hatchery trout did not reproduce ($R_h = 0$), the predicted total population size is significantly enhanced, especially at high fishing mortality (curve B). Under this circumstance, however, most of the population would consist

of first-generation hatchery fish, the wild component of the population having been effectively replaced (curve C). The shaded area indicates the magnitude of the loss of wild fish that occurs simply as a result of numerical displacement of the wild fish by the hatchery fish. Even at $F = 0.6$ and a total annual mortality rate of 50%, the loss of wild adults exceeded 90%. At this level of mortality, a sizeable wild stock was able to persist in the absence of stocking (curve A). The small gain in population size (about 12%) achieved by stocking, therefore, resulted in a 90% loss of the wild stock. When juvenile of the hatchery fish was set a half the survival rate of the wild fish, the enhancement effect of stocking five yearling trout ha^{-1} on the total population size was much less, even if the reproductive rate of the hatchery fish ($R_h = 1$) was equal to that of the wild fish (curve D). Under this reproductive and juvenile-survival scenario, the natural component of the population remains strong, but represents primarily the progeny of hatchery fish (curve B). In this case, there is a slight enhancement over the unstocked population (curve A), but only at fishing mortality rates exceeding $F = 0.6$ (curve B).

Low early survival - The effect of stocking on self-sustaining wild stocks of lake trout is even more dramatic when natural reproduction (i.e. survival from egg to yearling) is weak ($S_{wy} = 0.002$). In this situation (Fig. 58, lower panel), there was a significant enhancement of total adult population size, compared to the unstocked population (curve A), when $S_h = 1.0$ and $R_h = 0$ (curve B), but the wild fish were completely replaced by the hatchery fish even when fishing and total annual mortality rates were very low (curve C). Comparison of the shaded areas in Fig. 58 indicates that weakly reproducing wild stocks (lower panel) have much lower resistance to transformation by hatchery stocks than strongly reproducing wild stocks (upper panel). If the hatchery stock experiences reduced juvenile survival ($S_h = 0.5$), but reproduces at the same rate as the wild stock, there is significant enhancement of the total population size (Fig. 58, lower panel, curve D). The majority of the progeny, however, would originate from the hatchery versus wild fish, because the progeny of wild and hatchery fish were not tabulated separately.

The best-case stocking scenario is the one in which the hatchery fish do not reproduce because reproduction implies hybridization with the wild fish and complete loss of the wild stock through introgression. The percentage of known hatchery fish (i.e. fin clipped) under three reproductive scenarios is shown in the lower panel of Fig. 59. The upper two curves are for high survival of domestic juveniles ($S_j = 1$) and zero ($R = 0$) and full reproduction ($R = 1$) of the hatchery fish,

respectively. The lower curve is for low juvenile survival ($S_j = 0.5$) and full reproduction. When there is no reproduction by the hatchery fish, the percentage of clipped hatchery fish increases steeply with increasing fishing mortality. The percentage of clipped fish is much lower when there is natural reproduction of the hatchery fish. Depending on the fishing mortality and initial survival of the hatchery juveniles, the clipped fish comprise from about 5-60% of the population when natural reproduction of the hatchery fish occurs (Fig. 59, lower panel). The true representation of the hatchery contribution to the population is much greater, of course, because the new recruits originate primarily from hatchery fish, through either matings between hatchery fish or hybrid matings between hatchery and wild stock. It would seem likely that the actual percentage of wild fish would probably be fewer than indicated for the upper curve in the lower panel of Fig. 59, because some reproduction of hatchery fish would be expected. The only way to determine the actual contribution of the hatchery fish is to conduct a biochemical or cytogenetic analysis of an actual population.

Effects of Variable Stocking Rates

In the second set of simulations, the effect of varying the stocking rate from 1-5 yearling trout ha^{-1} was strongly dependent on juvenile survival and reproductive fitness of the hatchery fish (Table 30). The number and weight of wild fish in the population in the absence of stocking is 7974 fish and 5035 kg, respectively. The response to stocking is interpreted with reference to the unstocked population. For example, increase in the quantity of fish as a result of stocking is 118% at a stocking rate of 5 ha^{-1} , but only 36% at a stocking rate of 1 ha^{-1} when juvenile survival and reproductive success is equal to the wild stock. When juvenile survival is reduced to 0.5 and reproduction of the hatchery fish is zero, the increase in quantity is only 1 and 4% at stocking rates of 5 and 1 fish ha^{-1} , respectively. Survival of the juvenile hatchery fish in particular has large quantitative and qualitative effects on the population. For example, at a stocking rate of 5 ha^{-1} a 50% reduction in survival of the hatchery juveniles results in major reductions in the enhancement to the population as reproductive success declines from 1 to zero, respectively (Table 30). Reduction in juvenile survival also results in significantly fewer clipped fish in the population. At a low stocking rate of 1 ha^{-1} , a reduction in juvenile survival to 0.5 actually results in an increase in the enhancement to the population, when there is zero reproduction of hatchery trout, because of the positive effect of fewer adults of hatchery origin on reproduction of wild trout. The percentage of first generation (clipped) hatchery fish also declines dramatically when juvenile survival declines by 50%.

TABLE 30. Summary of the effects of variable stocking rates of hatchery-reared yearling lake trout on the standing stocks of clipped and unclipped adult trout age ≥ 6 yrs under varying juvenile survival and reproductive scenarios for the hatchery fish. The number of yearlings stocked corresponds to 5 ha⁻¹ (30,000), 3 ha⁻¹ (18,000) and 1 ha⁻¹ (6,000). Survival of stocked juveniles age 1, 2 and 3 yr is shown as a fraction of the survival of wild juveniles, which is determined by the stock recruitment function. Reproductive rate of the first generation hatchery fish is also shown as a fraction of the survival rate of wild fish which is fixed at 0.004 for egg to yearling stage. Unclipped fish include wild fish and the natural progeny resulting directly from reproduction of hatchery stock and from interbreeding between hatchery and wild fish. Simulations were run for 100 yr to achieve stable populations and numbers, and biomass of fish reported are means for years 76 to 100, inclusive. Fishing mortality was fixed at $F = 0.8$. Population enhancement is the increase over the wild unstocked population.

No. stocked	Survival of stocked juven.	Reprod. rate of stocked juven.	Unclipped			Stocked			Total population			Population enhancement numbers
			Status	No. ≥ 6 yr	Wt. ≥ 6 yr	Status	No. ≥ 6 yr	Wt. ≥ 6 yr	No. ≥ 6 yr	Wt. ≥ 6 yr	% of fish clipped	
0	-	-	Native wild	7,974	5,035	0	-	7,974	5,035	-	-	-
30,000	1.0	1.0	Natural progeny	10,052	6,248	Domestic	7,303	4,564	17,356	10,812	42	118
	0.5	0.5	Natural progeny	5,651	3,542	Domestic	8,168	5,138	13,819	8,680	59	73
	0	0	Native wild	248	158	Domestic	10,720	6,764	10,968	6,922	98	38
18,000	1.0	1.0	Natural progeny	8,475	5,363	Domestic	1,520	959	9,995	6,321	15	25
	0.5	0.5	Natural progeny	7,490	4,737	Domestic	1,630	1,028	9,120	5,765	18	14
	0	0	Native wild	6,234	3,941	Domestic	1,799	1,135	8,033	5,075	22	1
18,000	1.0	1.0	Natural progeny	9,257	5,804	Domestic	5,294	3,320	14,552	9,124	36	82
	0.5	0.5	Natural progeny	6,134	3,861	Domestic	5,924	3,730	12,058	7,592	49	51
	0	0	Native wild	1,241	786	Domestic	7,774	4,903	9,015	5,690	86	13
6,000	1.0	1.0	Natural progeny	8,392	5,311	Domestic	959	605	9,351	5,916	10	17
	0.5	0.5	Natural progeny	7,770	4,914	Domestic	1,013	639	8,783	5,553	12	10
	0	0	Native wild	7,043	4,454	Domestic	1,075	678	8,118	5,132	13	2
6,000	1.0	1.0	Natural progeny	8,610	5,445	Domestic	2,267	1,430	10,877	6,875	21	36
	0.5	0.5	Natural progeny	7,175	4,537	Domestic	2,483	1,567	9,659	6,104	26	21
	0	0	Native wild	5,096	3,222	Domestic	2,889	1,822	7,984	5,044	36	0
6,000	1.0	1.0	Natural progeny	8,330	5,269	Domestic	342	216	8,672	5,485	4	9
	0.5	0.5	Natural progeny	8,096	5,119	Domestic	350	220	8,446	5,339	4	6
	0	0	Native wild	7,901	4,995	Domestic	355	224	8,255	5,219	4	4

Selecting what would appear to be realistic rates of stocking (5 ha^{-1}) and juvenile survival (0.5), the model predicts an enhancement of only 14% at an instantaneous fishing mortality of 0.8, suggesting that stocking provides relatively marginal returns. Considering also the potential detrimental effects on the lake trout genetic resource it would seem of urgent importance to conduct a thorough evaluation of the objectives and practises of the lake trout stocking program.

SIMULATED RESPONSES OF LAKE TROUT TO VARIOUS DEVELOPMENT SCENARIOS

In this section, we used our population model to explore temporal changes in the abundance and biomass of adult fish for a lake trout population subjected to various hypothetical development scenarios. Three development scenarios have been modelled and illustrated here, but the model enables an infinite number of development variations to be explored. Each scenario begins with an undisturbed and unfished population. Mortality is sequentially increased on the population as roads, fishing, logging, dam construction, lodges, fishing guides, cottages, and other development-associated factors begin to operate on the lake trout population. The development scenarios are selected to encompass the range of stressors assumed to be operating on lake trout lakes in Ontario, although we have not attempted to verify the patterns or levels of mortality imposed in our hypothetical cases with actual examples.

The development scenarios impose two types of mortality on the simulated population: mortality on the adults through removal by fishing; and mortality of the early life stages (eggs and YOY) as a result of factors that degrade the quality of their habitat. Such factors, for example, might be: addition of silt to spawning areas and increased egg mortality; addition of nutrients and consequent degradation of both spawning and hypolimnetic summer nursery habitat; changes in water levels as a result of dams and water drawdowns with direct lethal effects on eggs and alevins; and direct loss of spawning habitat through shoreline modification.

Considerable information is available on the range of fishing mortality of lake trout in Ontario lakes (Fig. 53), but little information is available on the range of egg and YOY mortality of natural populations. Based on information on stock structure and the stock-recruitment relationship for the Lake Opeongo population, we have determined the approximate range of egg to yearling mortality by repeated simulations using the lake trout model. Using the approximate early survival rate determined for the Lake Opeongo population (0.003), we applied a 25% enhancement to simulate

pristine conditions and a 33% degradation to simulate loss of early life habitat. The degree of early mortality imposed in the simulations as a result of habitat loss due to development stress, therefore, would appear to be relatively conservative and within the realm of real possibility, notwithstanding the considerable uncertainty regarding early survival as noted.

In addition to factors that cause losses through mortality effects, we have simulated the effect of stocking hatchery-reared lake trout. Stocking was initiated in the simulation at a time corresponding to approximately a 50% depletion of the population and would probably correspond reasonably closely to the actual historical pattern of stocking in many Ontario lakes.

Description of Three Hypothetical Development Scenarios

The three development scenarios have been simulated, including moderate fishing, intensive fishing, and intensive fishing coupled with loss of early life habitat. The history of events associated with each of our three hypothetical development scenarios is outlined in Table 31.

Development causing moderate fishing - The first of our development scenarios imposes only a moderate fishing stress on the population and is designed to simulate the conditions that might be found in an area protected from development such as Algonquin Provincial Park. In this scenario, the population is completely undisturbed for the initial 20 yr, after which time road access is provided and a low fishing mortality is imposed. After another 10 yr have passed, knowledge of the fishery has spread and fishing mortality increases 2-fold, but because of seasonal regulations and controlled access, exploitation is held at this level indefinitely. Under this scenario, we assume no changes in habitat and no changes in early survival. The simulation is run for 100 yr to monitor changes in the population.

Development causing intensive fishing - The second development scenario incorporates a sequential increase in fishing mortality associated with the construction of an access road in year 20, a lodge with guides in year 30, and additional access and cottages in year 40. Fishing mortality increases in step-wise fashion from $F = 0.2$ in year 20 to $F = 1.0$ in year 50, after which time mortality is maintained at the latter level. Again habitat quality remains unchanged from pristine conditions during this development sequence, and early survival remains high for the duration of the simulation which is run for 100 yr.

TABLE 31. Three hypothetical development scenarios.

Development scenario,	History of development		Hypothesis/population parameters		
	Year	Events	Egg to age 1 yr		Adults (8-20 yr)
			S	M ₀	F
Moderate fishing	0	No access	0.004	5.5215	0.0
	20	Summer access road	"	"	0.2
	30	No further development and no winter fishing	"	"	0.4
	.	Status quo	.	.	.
	.	Status quo	.	.	.
	100	Status quo	0.004	5.5215	0.4
Intensive fishing	0	No access	0.004	5.5215	0.0
	20	Summer access road	"	"	0.2
	30	Lodge opened with guides	"	"	0.4
	40	Cottages constructed and	"	"	0.8
	50	winter fishing allowed	"	"	1.0
	.	Status quo	.	.	.
	.	Status quo	.	.	.
	100	Status quo	0.004	5.5215	1.0
Intensive fishing and habitat degradation	0	No access	0.004	5.5215	0.0
	20	Summer road construction	"	"	0.2
	30	Lodge opened with guides	"	"	0.4
	40	Logging, dam construction,	0.003	5.8091	0.8
	50	winter roads and cottages	"	"	1.0
	60	Marina and more cottages	0.002	6.2146	1.0
	.	Status quo	.	.	.
	.	Status quo	.	.	.
	100	Status quo	0.002	6.2146	1.0

Development causing intensive fishing and habitat degradation - In this scenario, the history of fishing development is identical to the intensive fishing scenario above, but reductions in early survival are superimposed on the population. Early survival is held constant at 0.004 from year zero to year 40 at which time survival declines 25% to 0.003. At year 60, early survival is reduced a further 25% to 0.002 from the pristine condition and remains at that level for the duration of the 100 yr simulation.

Population Responses to Exploitation and Habitat Loss

The three development scenarios outlined above represent a continuum from moderate to relatively extreme stress. Comparison of the temporal changes in population structure and abundance under the influence of these stressors reveals a corresponding gradation of response. The patterns of response of population density to moderate fishing, intensive fishing, and intensive fishing combined with habitat loss are shown in Fig. 60. Under moderate fishing pressure the total population size (age 1-20) declined by about 20%. There was an initial decline over a period of three decades as fishing mortality increased from zero to $F = 0.4$ (Fig. 60, Panel A). As fishing stress was imposed, there was a concomitant increase in the variation in total abundance. Over several decades of a fixed rate of moderate fishing, there was a gradual reduction in the variation in population abundance.

Under intensive exploitation, total population size declined to a much lower level appearing to stabilize at about year 90 following an 80% decline (Fig. 60, Panel B). With each new imposition of stress the population declined further, and continued to decline for about four decades following the final increase in fishing mortality at year 50. When habitat degradation and an associated reduction in early survival was added to the intense exploitation stress, the total population declined by 95% (Fig. 60, Panel C), which would place the population at a high risk of extinction.

Responses of adult (ages 6-20 yr) density (Fig. 61) and biomass (Fig. 62) of our hypothetical population to the three simulated levels of development stress paralleled those of total population density. The density and biomass of adults, however, was much more variable than total population density. The pattern of variation in both abundance and biomass was similar, variation increasing with imposition of stress and gradually diminishing over time at fixed levels of mortality (Fig. 61 and 62).

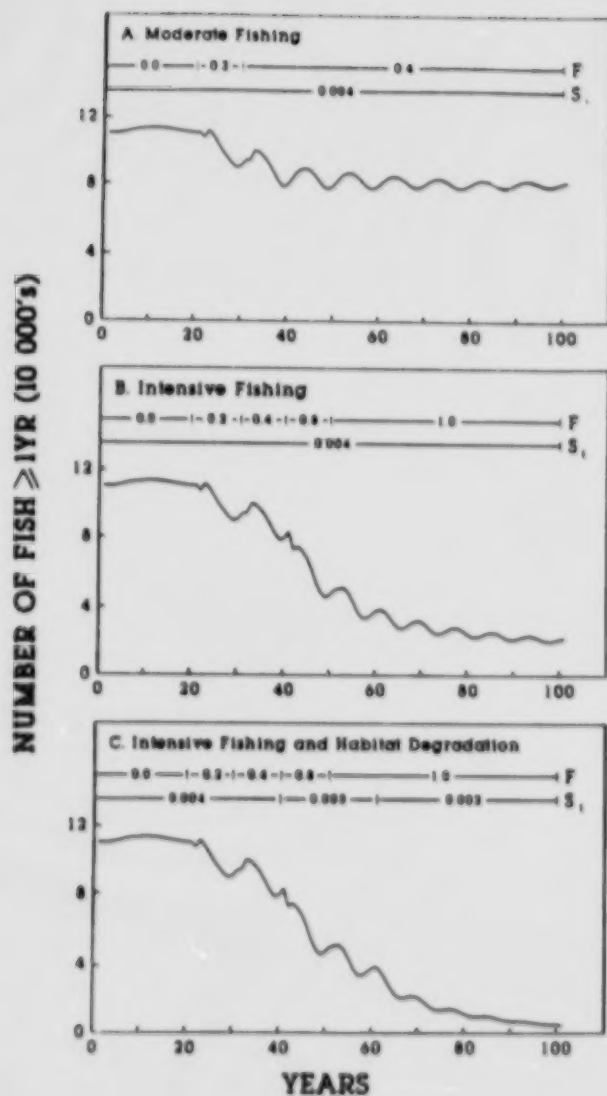


FIG. 60. The time course of simulated changes in total population size (trout 1-20 yr-old) of a hypothetical lake trout population in a 6000 ha lake under three development scenarios: moderate fishing (A), intensive fishing (B), and intensive fishing combined with habitat degradation. The levels and time course of changes in instantaneous fishing mortality (F) and early survival (S_1) are indicated at the top of each panel. The simulations were run for 100 yr.

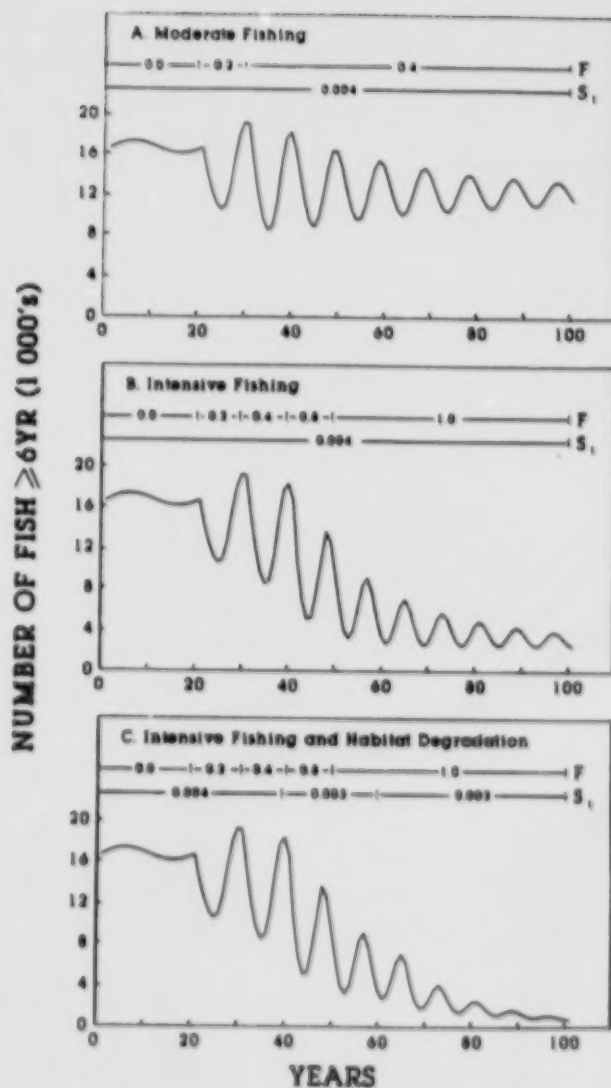


FIG. 61. The time course of simulated changes in adult population size (trout 6-20 yr-old) of a hypothetical lake trout population in a 6000 ha lake under three development scenarios: moderate fishing (A), intensive fishing (B), and intensive fishing combined with habitat degradation. The levels and time course of changes in instantaneous fishing mortality (F) and early survival (S_1) are indicated at the top of each panel. The simulations were run for 100 yr.

Under moderate fishing stress adult abundance and biomass declined about 25 and 52%, respectively (Fig. 61 and 62, Panel A), with a significant decline in mean body size of the fish. Intensive fishing resulted in about 82 and 90% declines in abundance and biomass, respectively, of the adult fish (Fig. 61 and 62, Panel B). Intensive fishing combined with habitat loss and reduced early survival (egg to yearling) resulted in 94 and 97% declines in number and biomass, respectively, of adult trout (Fig. 61 and 62, Panel C).

The effects of our hypothetical development scenarios on population structure include the loss of older fish from the population and in particular the loss of adults of reproductive age (Fig. 63). At moderate fishing intensity, trout up to 20 yr of age persist in the population, whereas under intensive fishing mortality, the maximum age attained is 14 yr with only one or two 14 yr-olds appearing in the population from years 60 to 100 of the simulation (Fig. 63). Intensive fishing combined with reduced early survival resulted in a further reduction of the number of adult fish and the maximum age declined to 12 yr. Under moderate fishing stress the number of mature adults declined by 17% from the unexploited population structure (Fig. 51a). Under intensive fishing stress, the number of mature adults declined a further 74% from the moderately fished population structure and under the intensive fishing and habitat loss scenario the mature adults declined 89% from the moderately fished population structure.

Responses of Stressed Lake Trout Populations to Stocking

In this section, we explore the effects of stocking yearling lake trout on the population density and biomass of a severely stressed lake trout population. The development scenario chosen is the one involving intensive exploitation and habitat loss (Table 31). Three stocking scenarios are evaluated using stocking rates of 1, 3, or 5 yearling lake trout ha^{-1} . In each simulation we have assumed that natural reproduction occurs and that the reproductive success of the hatchery trout is the same as for the wild trout. Two survival rates have been tested for the juvenile hatchery trout, however, survival was set at either the same rate for both wild and hatchery juveniles, or hatchery juveniles were set at one half the survival rate of wild juveniles. In each case, the hatchery yearlings were injected into the population at year 50 of the simulation and the simulation was continued for an additional 50 yr.

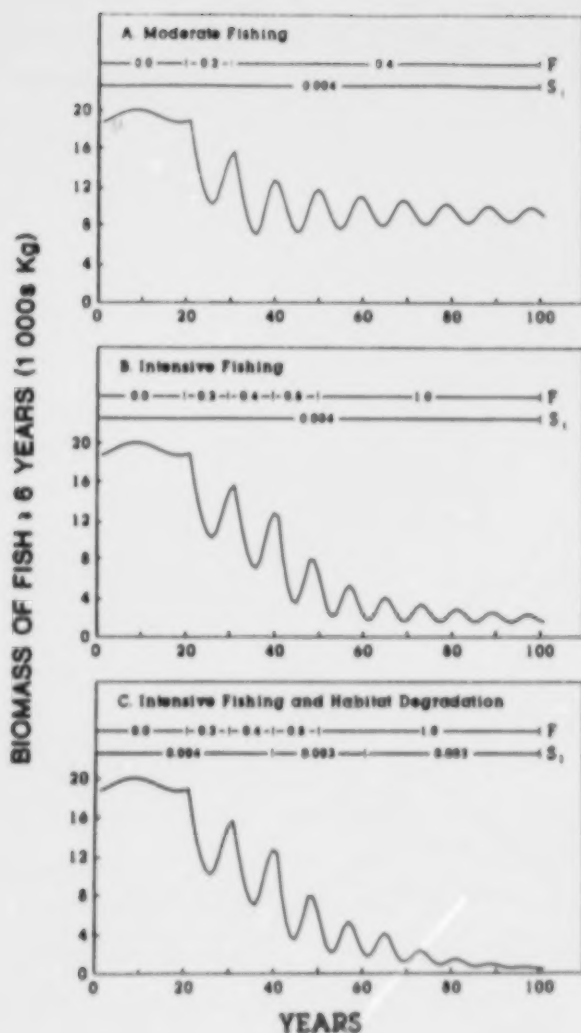


FIG. 62. The time course of simulated changes in adult population biomass (trout 6-20 yr-old) of a hypothetical lake trout population in a 6000 ha lake under three development scenarios: moderate fishing (A), intensive fishing (B), and intensive fishing combined with habitat degradation. The levels and time course of changes in instantaneous fishing mortality (F) and early survival (S_i) are indicated at the top of each panel. The simulations were run for 100 yr.

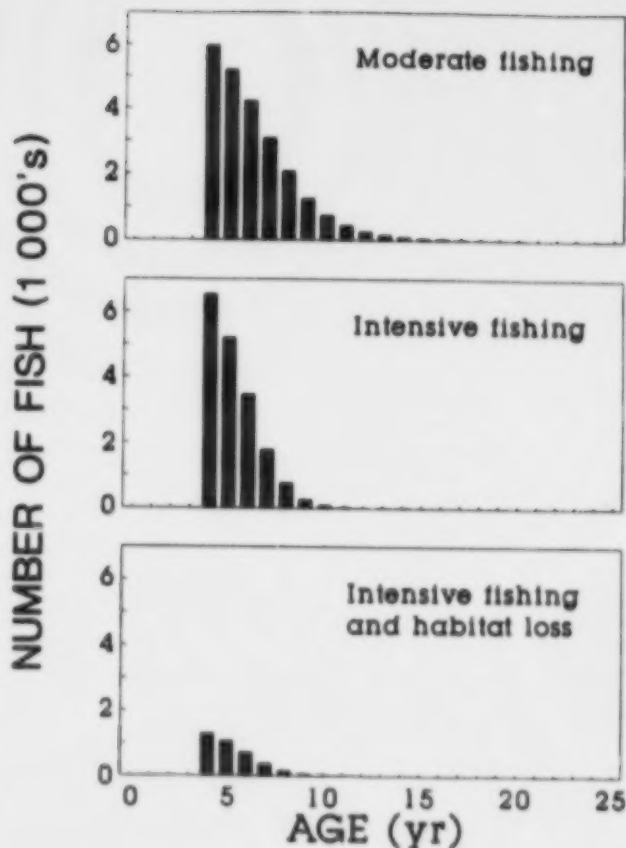


FIG. 63. Age frequency distributions of lake trout age 4-20 yr in a hypothetical lake trout population in a 6000 ha lake under three simulated development scenarios: moderate fishing, intensive fishing, and intensive fishing with habitat degradation as in Fig. 60, 61, and 62.

The response of the population to stocking is markedly influenced by the number of yearlings released and by the survival of the hatchery fish during their first 3 yr in the lake (Fig. 64). At the highest stocking rate (30,000 yearlings yr^{-1}) and the higher level of juvenile survival, release of hatchery yearlings can restore the total population density (age 1-20 yr) to above the pre-exploitation level. If survival of the hatchery juveniles is 0.5 of the wild juveniles, however, the enhancement is reduced by 40% (Fig. 64, upper panel). At stocking rates of 18,000 and 6000 yearlings yr^{-1} , the total population is enhanced to 80 and 55%, respectively, of the unexploited level when survival of the wild and hatchery-reared juvenile trout is equal, but only 55 and 18% when survival of the hatchery-reared juveniles is 0.5 of the wild fish (Fig. 64, middle and lower panel).

Enhancements in the quantity of adult trout due to stocking is not as great as it is for trout of younger ages, but the variability (cyclicality) introduced is much greater as the density-dependent regulatory mechanism over- and undercompensates in response to injections of yearling fish (Fig. 65). When the survival of juvenile hatchery-reared trout is the same as the wild trout, stocking of 30,000, 18,000 and 6000 yearlings results in 76, 61, and 38% restoration of the unexploited population density, respectively. When juvenile survival of hatchery yearlings is 0.5 of the rate for the wild fish, the enhancements due to stocking are only 30, 23, and 15% of the unexploited levels (Fig. 65).

The changes in adult biomass with variation in stocking rate simply parallel the changes in population density (Fig. 66), but the actual percentage gains are much smaller. When juvenile survival is the same for wild and hatchery trout, the enhancement as a result of stocking 30,000, 18,000, and 6000 yearlings is 40, 30, and 20% of the unexploited stock, respectively, compared to about 16, 10, and 7% when survival of hatchery-reared juveniles is 0.5 of the survival rate for the wild trout.

The above simulations suggest that, under some circumstances, stocking of hatchery-reared lake trout can have a major influence in restoring and maintaining densities of lake trout under relatively severe stress. The enhancement is partly illusory, however, in that young age groups will dominate the population, as reflected by the modest enhancement in adult biomass. The simulations also indicate the critical importance of the level of juvenile survival of the hatchery-reared trout. Improvements to the quality of hatchery fish, and stocking practises that enhance juvenile survival, would probably significantly improve the effectiveness of stocking hatchery-reared yearlings. This

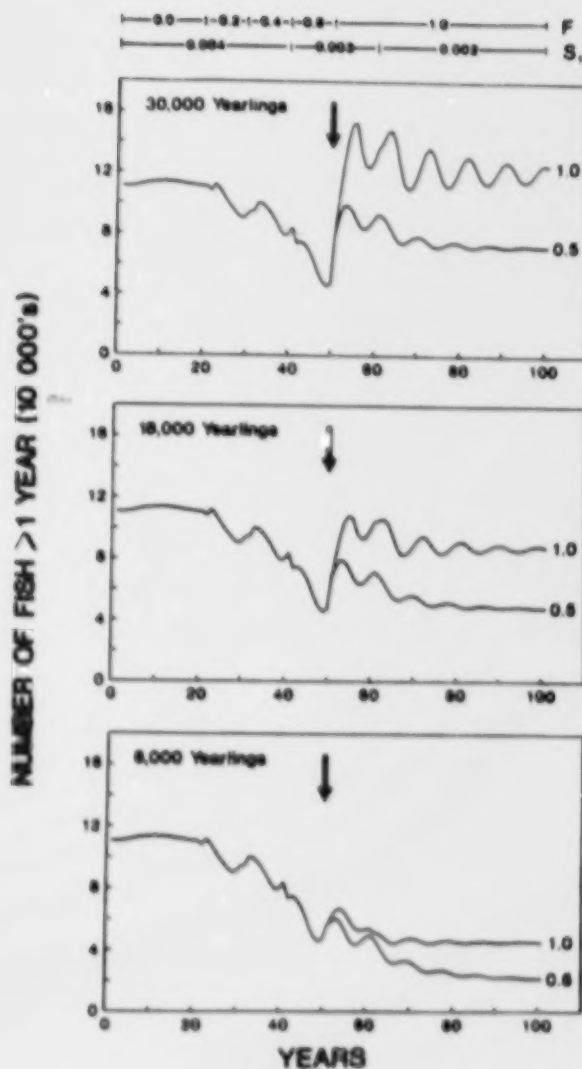


FIG. 64. The time course of simulated changes in population size (ages 1-20 yr) of a severely stressed lake trout population in a hypothetical 6000 ha lake subjected to three rates of stocking of hatchery-reared yearling lake trout. The levels of instantaneous fishing mortality and early survival are shown at the top of the figure and correspond to development scenario C in Figs. 60, 61, and 62. Stocking of hatchery trout was initiated at year 50 of the simulation, indicated by the vertical arrow, and was continued annually at the indicated rate for the duration of the 100 yr simulation. Two rates of juvenile survival were simulated for the first generation hatchery trout: survival equal to that for the wild juveniles (1.0) and survival equal to one half that for the wild juveniles (0.5).

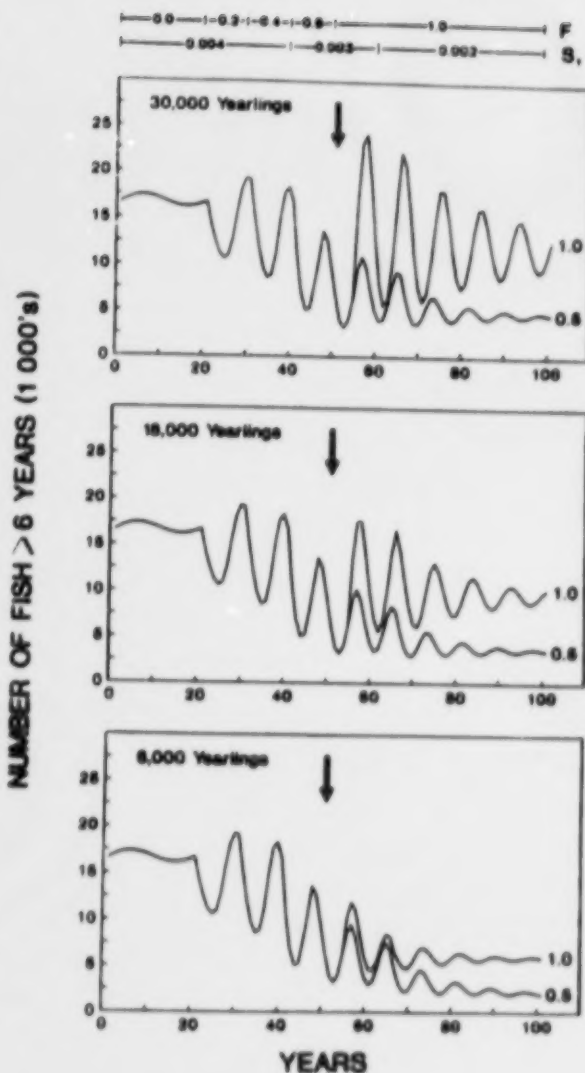


FIG. 65. The time course of simulated changes in adult population size (ages 6-20 yr) of a severely stressed lake trout population in a hypothetical 6000 ha lake subjected to three rates of stocking of hatchery-reared yearling lake trout. The levels of instantaneous fishing mortality and early survival are shown at the top of the figure and correspond to development scenario C in Figs. 60, 61, and 62. Stocking of hatchery trout was initiated at year 50 of the simulation, indicated by the vertical arrow, and was continued annually at the indicated rate for the duration of the 100 year simulation. Two rates of juvenile survival were simulated for the first generation hatchery trout: survival equal to that for the wild juveniles (1.0) and survival equal to one half that for the wild juveniles (0.5).

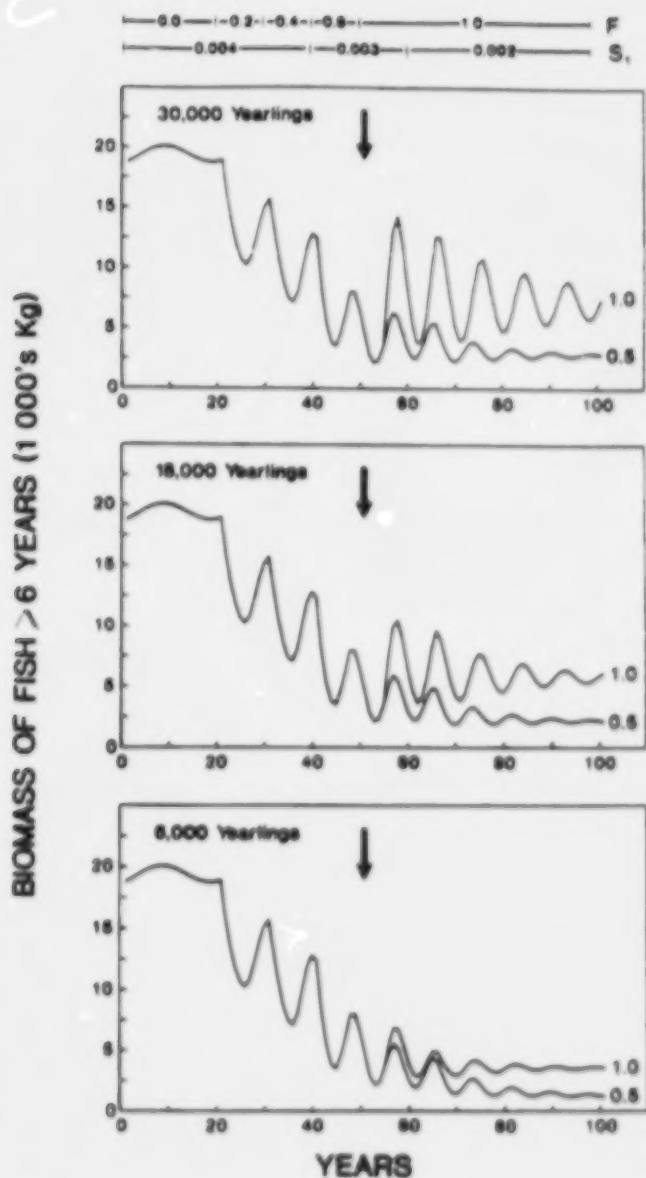


FIG 66. The time course of simulated changes in adult population biomass (ages 6-20 yr) of a severely stressed lake trout population in a hypothetical 6000 ha lake subjected to three rates of stocking of hatchery-reared yearling lake trout. The levels of instantaneous fishing mortality and early survival are shown at the top of the figure and correspond to development scenario C in Figs. 60, 61, and 62. Stocking of hatchery trout was initiated at year 50 of the simulation, indicated by the vertical arrow, and was continued annually at the indicated rate for the duration of the 100 yr simulation. Two rates of juvenile survival were simulated for the first generation hatchery trout: survival equal to that for the wild juveniles (1.0) and survival equal to one half that for the wild juveniles (0.5).

must be tempered, however, by the knowledge that hatchery-reared trout can have a major influence on the genetic composition of the stocked population, although, the problem of genetic transformation of native stocks could be largely avoided by ensuring the use of local stocks and use of scientifically sound breeding and rearing practices. Even under ideal circumstances, however, stocking provides relatively small gains in numbers of fish and serves primarily to sustain very high fishing intensity and to mask the serious overexploitation of wild stocks.

REHABILITATION OF LAKE TROUT POPULATIONS

Detailed discussion of rehabilitation of degraded lake trout populations is beyond the scope of this synthesis, but some discussion of this aspect is warranted, especially in terms of the prognosis for recovery of degraded stocks. The potential scope for mitigation of stress effects for achieving rehabilitated lake trout communities is enormous over the range of stress effects that we have considered, but only a few of these are solely within the realm of fisheries management. Two of the most important stressors, however, are readily amenable to fisheries management control. These are regulation of harvest, and stocking of hatchery-reared lake trout. Two rates of juvenile survival were simulated for the first generation hatchery trout: survival equal to that for the wild juveniles (1.0) and survival equal to one half that for the wild juveniles (0.5).

In this section, we address the question of management options for rehabilitation of heavily exploited and stocked lake trout stocks. Our third development scenario (i.e. intensive fishing and degradation of early-life habitat) has been used as the system state requiring rehabilitation. We have used our lake trout model to simulate the pattern and time frames for various rehabilitation strategies. Fish community changes would be expected to occur in concert with a decline in a lake trout stock and these changes might well prevent a simple reversal of lake trout population trends when stressors are removed. For example, Gunn et al. (1987) found that the abundance of other hypolimnetic fish species influenced the success of stocked lake trout in recovering acidified lakes. The recovery responses of our hypothetical, degraded lake trout population to various rehabilitation scenarios must be considered as best possible cases. Nonetheless, we expect that the simulated responses under our rehabilitation strategies should reveal their relative potential effectiveness.

Five hypothetical rehabilitation scenarios were simulated as follows:

- a total moratorium on fishing for an indefinite period;

- a reduction in fishing mortality to $F = 0.4$;
- a reduction in fishing mortality to $F = 0.4$ and rehabilitation of spawning and nursery habitat with a 33% improvement in early survival;
- a 10 yr closure of the fishery with a reduced fishery at $F = 0.4$ thereafter; and
- a 5 yr closure of the fishery, stocking of yearling lake trout ($5 \text{ ha}^{-1}\text{yr}^{-1}$) of the same or well matched stock during the first 2 yr of the closure, and reestablishment of a reduced fishery in year 6 at $F = 0.4$.

Each rehabilitation scenario was run for an additional 100 yr following 100 yr of intensive fishing and habitat degradation (development scenario 3, Fig. 60C). The strongest response occurred when a complete moratorium on fishing was imposed (rehabilitation scenario 1). Despite persistence of the reduced early survival, the population recovered to a new stable adult stock size of 12,000-14,000 adult fish (6 yr and older), but 20 years were required to reestablish an equilibrium population (Fig. 67 and 68) and a stable age structure was achieved by year 30 (Fig. 69). When fishing intensity was reduced to $F = 0.4$ (scenario 2), the adult stock gradually increased to about 6500 fish over a period of about 50 yr, although 5000 adults were present after 27 yr (Fig. 67), and a much broader age structure was also achieved (Fig. 70). Rehabilitation scenario 3, with reduced fishing intensity to $F = 0.4$ and habitat rehabilitation, resulted in a stable population of about 10,000 adults after about 45 yr, although most of the increase had occurred by year 25 (Fig. 67 and 68), and a broader age structure and enhanced longevity was achieved by year 30 (Fig. 71). The notable feature of each of these scenarios is the lengthy time intervals required to reestablish equilibrium populations (25-50 yr).

A more realistic management question is to ask what is the most effective and timely way to reestablish a stable, fishable population that can provide a satisfactory yield of wild trout. Based on the Lake Opeongo experience, we have assumed that a comparable population could sustain a fishing mortality of $F = 0.4$ (see Fig. 51 and 61). In rehabilitation scenario 4, a population of about 8000 adult lake trout was achieved after 10 yr of closure of the fishery. After reopening of the fishery at $F = 0.4$, the adult stock declined to a low of 5300 fish within 5 yr, and stabilized at about 6500 fish thereafter (Fig. 72). Associated changes in biomass are shown in Fig. 73. By year 10, many old fish (> 10 yr) were present, but these were removed when the fishery reopened and a relatively stable age structure was achieved by year 30 (Fig. 74). In rehabilitation scenario 5, the adult stock increased to about 9000 fish and 7000 kg after 5 yr of closure of the fishery (Fig. 72 and 73). After reopening

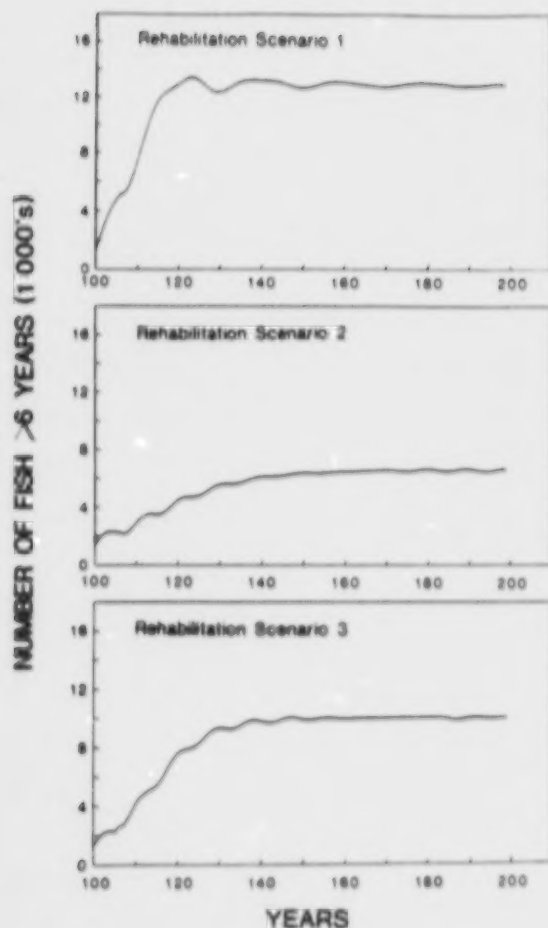


FIG 67. Time course of simulated changes in the abundance of adult lake trout in a severely stressed population in a hypothetical 6000 ha lake subjected to three different rehabilitation scenarios: (1) a complete closure of all fishing; (2) reduction of instantaneous fishing mortality to 0.4; and (3) reduction of instantaneous fishing mortality to 0.4 plus increase in early survival by 33% through habitat rehabilitation. Rehabilitation was initiated at year 100 of development scenario C, illustrated in Figs. 60, 61, and 62.

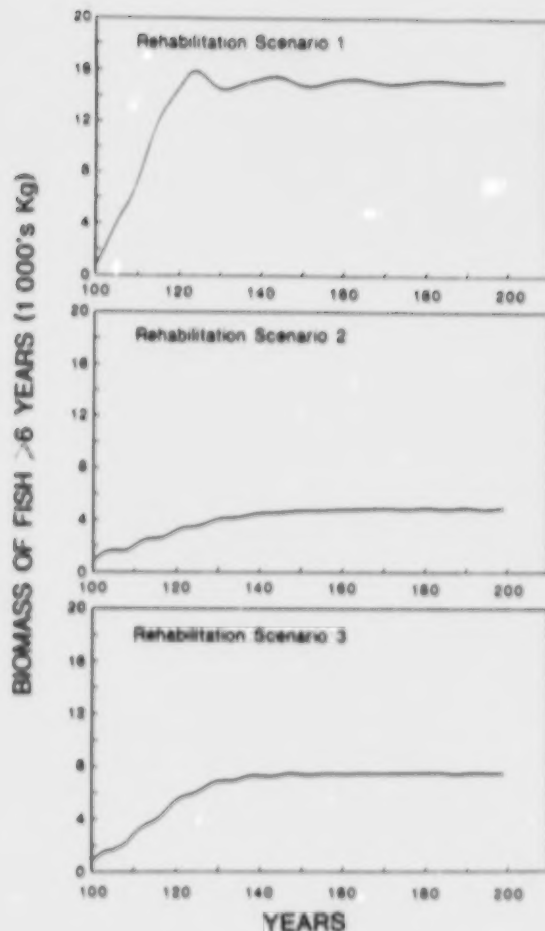


FIG 68. Time course of simulated changes in the biomass of adult lake trout in a severely stressed population in a hypothetical 6000 ha lake subjected to three different rehabilitation scenarios: (1) a complete closure of all fishing; (2) reduction of instantaneous fishing mortality to 0.4; and (3) reduction of instantaneous fishing mortality to 0.4 plus increase in early survival by 33% through habitat rehabilitation. Rehabilitation was initiated at year 100 of development scenario C, illustrated in Figs. 60, 61, and 62.

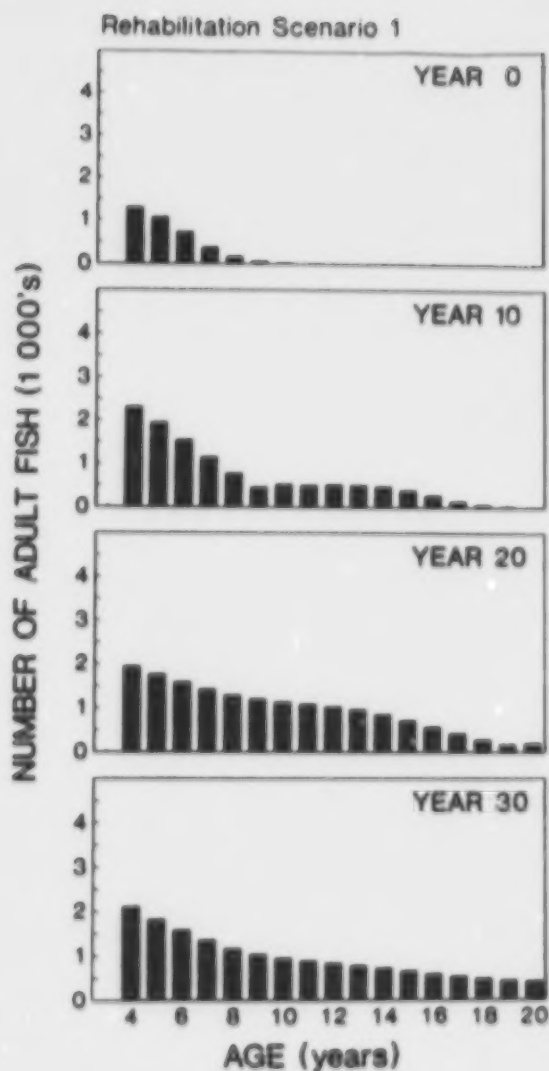


FIG. 69. Changes in the abundance of lake trout age 4-20 yr at 10 yr intervals for the first 30 yr following initiation of rehabilitation scenario [1] (Fig. 67).

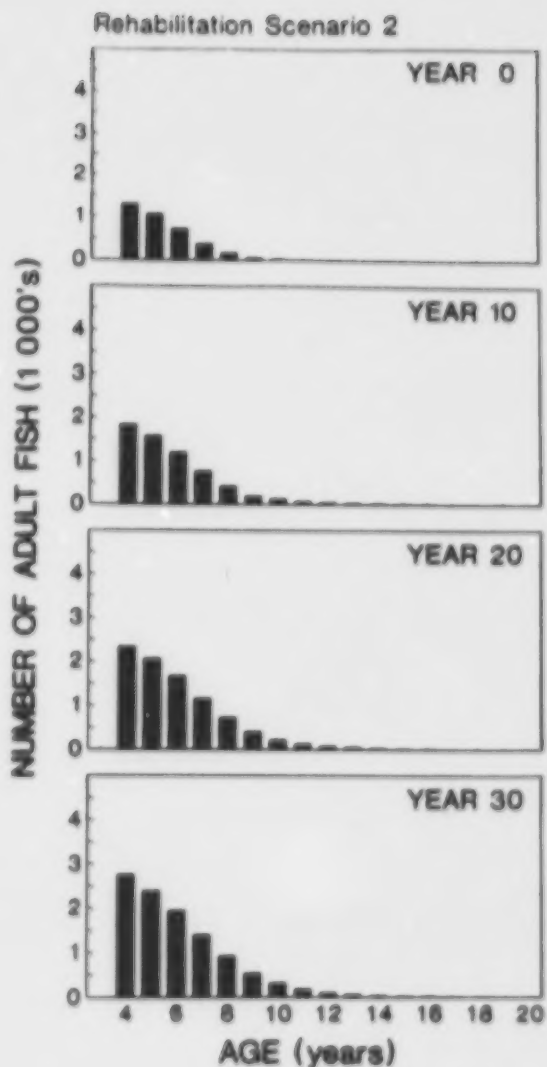


FIG. 70. Changes in the abundance of lake trout age 4-20 yr at 10 yr intervals for the first 30 yr following initiation of rehabilitation scenario [2] (Fig. 67).

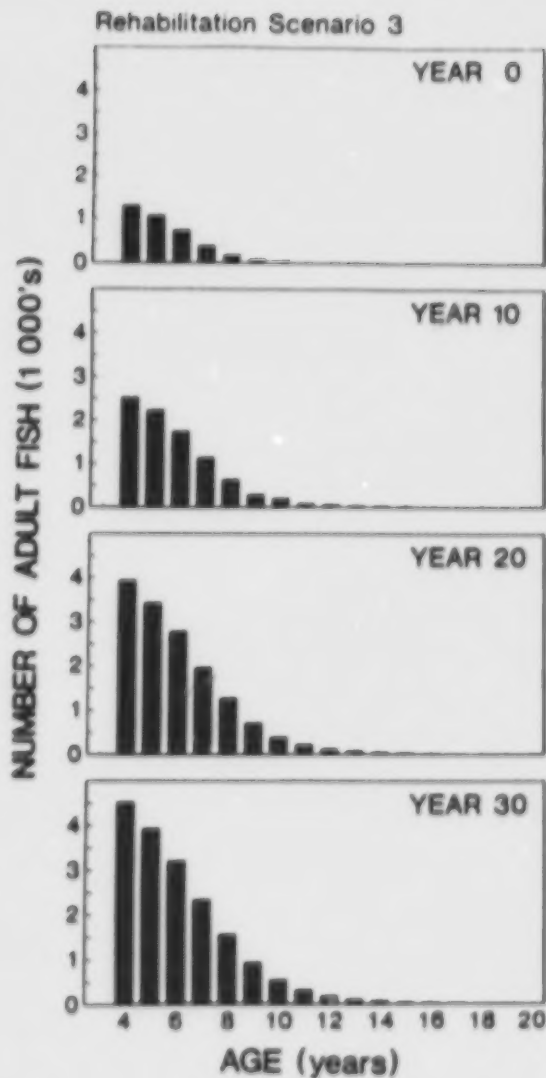


FIG. 71. Changes in the abundance of lake trout age 4-20 yr at 10 yr intervals for the first 30 yr following initiation of rehabilitation scenario [3] (Fig. 67).

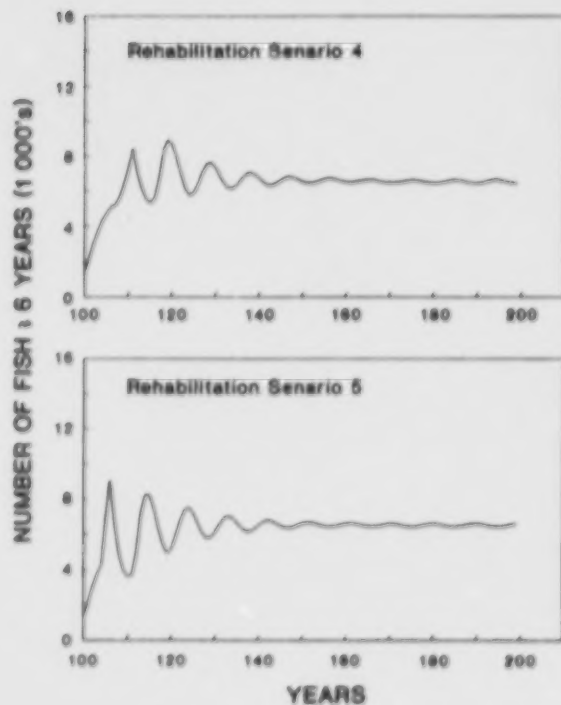


FIG. 72. Time course of simulated changes in the abundance of adult lake trout in a severely stressed population in a hypothetical 6000 ha lake subjected to two different rehabilitation scenarios: [4] a 10 yr closure of all fishing, followed by restoration of fishing at a reduced instantaneous mortality rate of 0.4; and [5] a 5 yr closure of all fishing with stocking of 30,000 (5 ha⁻¹) yearling lake trout in each of the first two years of the closure, followed by reopening of fishing at a reduced instantaneous fishing rate of 0.4. Rehabilitation was initiated at year 100 of development scenario C, illustrated in Figs. 60, 61, and 62.

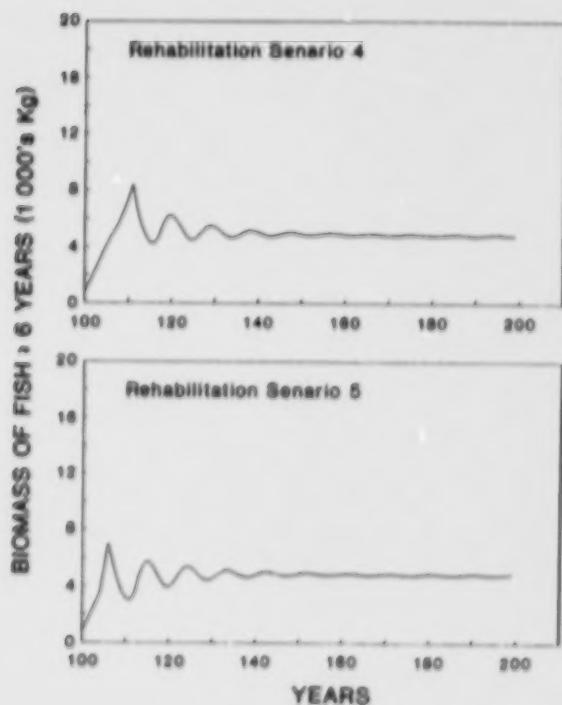


FIG. 73. Time course of simulated changes in the biomass of adult lake trout in a severely stressed population in a hypothetical 6000 ha lake subjected to two different rehabilitation scenarios: [4] a 10 yr closure of all fishing, followed by restoration of fishing at a reduced instantaneous mortality rate of 0.4; and [5] a 5 yr closure of all fishing with stocking of 30,000 (5 ha^{-1}) yearling lake trout in each of the first two years of the closure, followed by reopening of fishing at a reduced instantaneous fishing rate of 0.4. Rehabilitation was initiated at year 100 of development scenario C, illustrated in Figs. 60, 61, and 62.

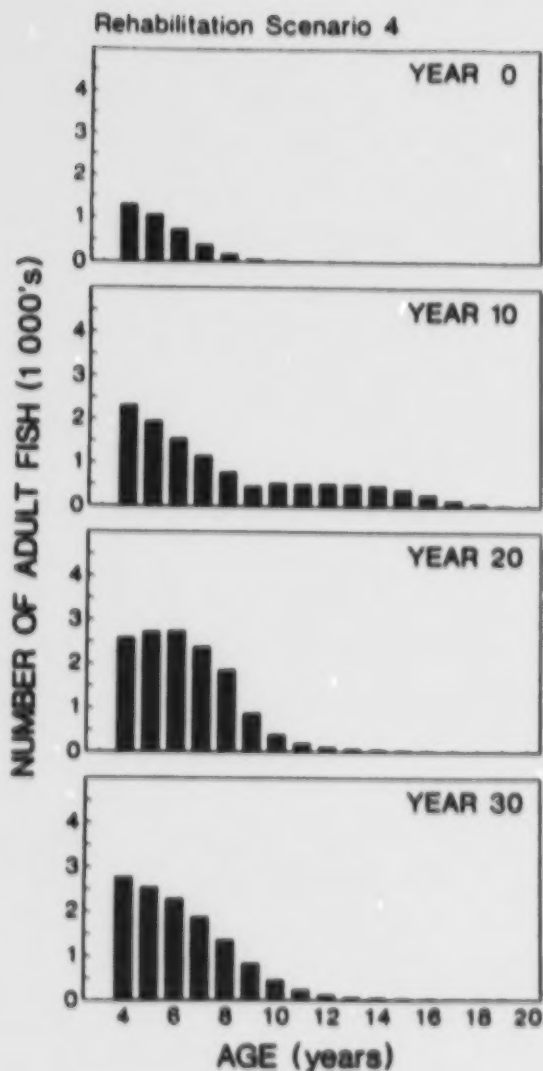


FIG. 74. Changes in the abundance of lake trout age 4-20 yr at 10 yr intervals for the first 30 yr following initiation of rehabilitation scenario [4] (Fig. 72).

of the fishery, the adult stock fell to a low of 3600 fish 5 yr later, but eventually stabilized at 6000-7000 adult lake trout (5000 kg) by about 25 yr after the initial closure (Fig. 72 and 73). Again, a relatively broad and stable age structure was attained by year 30 (Fig. 75).

Our lake trout model enables preliminary exploration of possible rehabilitation strategies through computer simulation. We emphasize that the results of the simulations should be taken only as best case predictions. Also, we caution that the model would be expected to perform best for stocks similar to the Lake Opeongo stock upon which it is based. We have already noted the possibility of fish community changes at very high or low lake trout densities that might alter the stock recruitment relationship of any given population. Nevertheless, the model provides a first order resolution of the possible time frames involved in reversal of a chronic lake trout population decline, due to intensive exploitation and habitat degradation.

The five rehabilitation scenarios presented above demonstrate the types of management options that could be explored through simulation. The simulations also illustrate the lengthy time frames that will likely be involved and suggest the management commitment that will be required to restore self-sustaining stocks of lake trout after decades of chronic decline.

DISCUSSION AND MANAGEMENT IMPLICATIONS

EXPLOITATION STRESS

Angling exploitation of lake trout populations operates as a stressor, because members of the fish population are killed. Natural populations can accommodate considerable fishing mortality, however, before the stress of fishing begins to have a detrimental effect on lake trout production. Some fishing mortality will have a beneficial effect on total production, as slower growing, larger fish are removed and, subsequently, replaced by faster growing, younger fish. Surplus production, therefore, is maximized at a level (MSY) below maximum stock density. As fishing mortality increases and catch exceeds MSY, however, production declines. The number of recruits will continue to decline (Fig. 57), and mean body size and population biomass will decline as fishing mortality increases further (Fig. 52). The fishing mortality at which recruitment (age 4 yr) is maximized within any given habitat, signals the point at which exploitation mortality begins to overtake the compensatory capacity of the

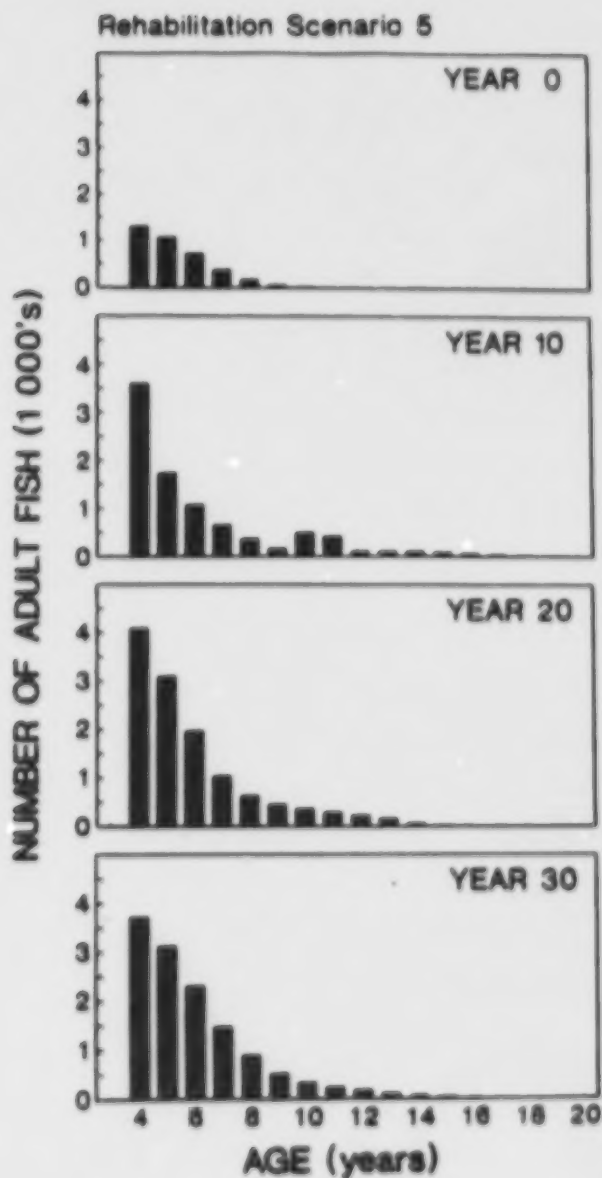


FIG. 75. Changes in the abundance of lake trout age 4-20 yr at 10 yr intervals for the first 30 yr following initiation of rehabilitation scenario [5] (Fig. 72).

population, and reproductive success declines. At that point, exploitation will have caused sustainable yield in kilograms to decline well below MSY. However, this will occur before the maximum recruitment level is reached, because MSY is a function of both recruitment and growth rate (see Payne et al. 1990).

We classified lake trout yields according to the relative concern of overexploitation, the latter being defined as a rate of fishing and fish removal that causes changes in the abundance of mature fish sufficient to lower the natural productive capacity below that required to achieve optimum yield. In our classification scheme, "optimal yield" was simply determined empirically as the observed range (0.20-0.75 kg ha⁻¹yr⁻¹) of long-term sustainable yields. We found that about one half of the lake trout fisheries in our annual-harvest data set exceeded the 0.75 kg ha⁻¹yr⁻¹ threshold. Of the fisheries exceeding this guideline, those in the two highest categories of concern (i.e. 9 and 10, Fig. 14), in many cases, involved stocked populations (Fig. 13). This was also true for winter and open-water fisheries (Fig. 8 and 12), although in all seasons, wild stocks were well represented in the high concern categories.

Use of Two Fishing Lines During Winter

We have reported winter fishing effort, in terms of rod-hours and angler-hours, because of uncertainty about the effectiveness of using one versus two lines, and because of the variable use of two lines. Lester et al. (1991) evaluated the effectiveness of one versus two lines and found that variation, due to number of rods per angler, were not significant when averaged across lakes. They also noted, however, that the effects for individual lakes varied from doubling to actually decreasing catch rates as the number of rods was doubled.

Theoretically, we would expect the effect of two rods per angler to be greater on small lakes, which have lower habitat diversity than large lakes and, therefore, more evenly dispersed fish populations, which are also more easily located by fishermen. Encounter probabilities between fish and fishing lures would be expected to be more directly a function of the number of rods employed in these lakes. Also, in small lakes with less complex fish communities, it is more likely that both rods of a pair deployed by an angler would be targeted at lake trout. Data presented by Lester et al. (1991, Appendix B) indicate that two rods doubled catch rates per angler in 19.4% of the cases examined, and that this effect was observed only on the smaller lakes.

Effect of Lake Size

Lake size exerts two primary effects on harvest of lake trout. The first and dominant effect is due to scale, large lakes simply produce more fish than small lakes. The second effect of size is due to variation in lake productivity, small lakes being inherently more productive than large lakes. The first effect is clearly demonstrated by our analyses. Fishing effort, which is the primary driver of harvest, accounts for most of the scale effect and for most (about 70-80%) of the total variation in harvest. The productivity effect was seen for winter (rod-hours only, Table 3) and annual harvests (Table 7), accounting for an additional 9 and 4% of the variance in harvest in weight. Also, in both cases, the $\log_{10}$ regression coefficients were <1 (0.42 ± 0.13 ; 0.29 ± 0.09), indicating declining harvests in weight per unit area as lake size increased. In both cases, HUE increased with lake size, but this is possibly due to our comparison of lakes at different stages of exploitation development, small lakes being more intensively fished.

Fishing intensity is excessive on small lakes during all seasons, but especially during winter. The critical lake size at and below which excessive yield (with reference to the $0.75 \text{ kg ha}^{-1}\text{yr}^{-1}$ guideline) occurred during winter was 1008 ha (95% confidence interval: 694-1463 ha). Harvest controls appear to be needed on lakes ≤ 1000 ha, if self-sustaining status is to be maintained.

Productivity and Habitat

Yields for lake trout angling fisheries are influenced by lake productivity, and availability and quality of habitat. Yield was negatively correlated with MEI and TDS, and positively correlated with the amount of deep-water (>30 m) habitat. TDS appears to be acting as a surrogate of habitat quality rather than a productivity factor. TDS would be expected to be positively correlated with primary production and, in turn, would be negatively correlated with spawning and nursery habitat quality, possibly explaining its negative correlation.

There is a need to better understand the effect of productivity on lake trout yields, especially as this is related to lake size. At present, we have adopted common yield guidelines (Fig. 8-13) for all lakes, irrespective of lake size. This aspect clearly requires further research, because yield is not independent of lake size.

Degradation of spawning and juvenile nursery habitats will have major effects on lake trout production dynamics, as suggested by the importance of nursery habitat volume on observed yields (Table 14), and as revealed by our computer simulations (Fig. 61-63). No degradation or loss of these habitats can be allowed, if wild, self-sustaining lake trout production and yields are to be maintained at present levels. Rehabilitation of these habitats, where degradation has already occurred, would be expected to enhance lake trout production, provided that adequate escapement of mature adult fish is permitted.

Seasonal Fishing Patterns

Fishing pressure on lake trout stocks is greatest during winter, fishing intensity in rod-hours ha^{-1} being 4.8- and 2.1-times greater than during spring and summer seasons, respectively. Fishing intensity in angler-hours ha^{-1} is about 25% higher during winter than during open-water seasons. Estimated yields (kg) for all lake sizes are similar during winter and open-water seasons. HUE in weight is 27% higher during summer, but average HUE in number of fish is 39% higher during winter (Table 15). The mean duration of the winter fishing season was 86 d compared to 151 d for the open-water season, thus, much more fishing effort and a comparable harvest was concentrated during the winter season, indicating the popularity of these fisheries.

Winter fisheries harvest more small, immature fish than open-water fisheries (Table 15, mean weight (kg): winter 0.50; open-water 0.89). Harvesting immature trout can have a dramatic effect on the reproductive capacity of a lake trout population (Payne et al. 1990). High rate of harvest of immature fish during winter, therefore, has the potential to seriously impair the production and viability of lake trout stocks. Many of the lake trout lakes (74%) in our winter data set have received supplemental stocking of hatchery-reared lake trout, which suggests that many wild stocks have been depleted. Assessment of individual lake case histories would be required to determine the causes of decline, but overexploitation would be a primary suspect given the high yields associated with stocked lakes, especially during winter (Fig. 8).

Predicting yields between seasons - Equations were presented (Table 17) for predicting fishing intensities and yields for a particular season (winter, spring, summer, etc.) from effort or yield from another season for the same lake. This method could be used to provide an approximate estimate for annual yield when information was available for only one or two seasons.

Stocking of Lake Trout

Relative reproductive success tends to be lower in hatchery-reared lake trout, but little is known about behavioural and reproductive interactions between hatchery and native stocks, although it is suspected that interbreeding occurs. Transplanted stocks appear to be less fit than native stocks, even less than hatchery-reared native stocks. One Ontario study has clearly shown less genetic variability in transplanted lake trout stocks (Ihssen et al. 1988).

Even in the absence of reproduction of introduced stocks or interbreeding of introduced stocks and native stocks, stocking of hatchery-reared lake trout can lead to loss of the native gene pool. This will occur when artificial recruitment exceeds natural recruitment, and is greatly accelerated at high exploitation rates. There is a synergism between stocking and exploitation that accelerates the effect of introduced stocks on native stocks, whereby high exploitation causes stock depletion, leading to stocking being initiated. Stocking, in turn, stimulates more, or at least sustains, fishing pressure at rates in excess of the capacity of natural production systems to provide new lake trout recruits. In the extreme, exploitation could possibly remove all mature fish, preventing any natural recruitment, in which case, the wild stocks would be replaced by hatchery stock within one generation. Our simulation model clearly demonstrated the dramatic loss of wild fish due to stocking and exploitation, even when reproduction of the hatchery fish is zero (Fig. 58 and 59). When reproduction of the domestic fish occurs, the loss of wild fish is masked, because unclipped progeny of the domestic stock appear to represent wild fish (Fig. 59). The actual status of a wild population that has been supplemented by stocking is not readily apparent, therefore, unless the reproductive ecology is known (i.e. the extent of reproduction and interbreeding) and a simulation modelling approach is employed. Alternatively, biochemical genetic techniques could be employed, provided the genetic structures of the wild and introduced stocks were known (Allendorf and Phelps 1981). The present model, however, provided a clear indication of the probable magnitude of the transformation that is likely to occur at various rates of fishing and stocking. Application of the model to the stocking history of Lake Manitou, Ontario, from 1952-1989 predicted very closely the actual decline in the percentage of wild lake trout in the fall spawning run (Evans and Wilcox 1991).

HABITAT DEGRADATION

Lake trout populations are more abundant in low productivity, deep, well oxygenated lakes (Martin and Olver 1976). Our findings have revealed that well oxygenated summer nursery habitat

in deep water is an important habitat requirement for strong self-sustaining populations. Wild self-sustaining stocks are only found where an adequate habitable lake volume (i.e. temperature $<15.5^{\circ}\text{C}$ and dissolved oxygen $>2.0\text{ mg L}^{-1}$) is available (Fig. 37). Significant correlations between nursery habitat (positive effect), TDS (negative effect) and yields of lake trout suggest that a critical factor for self-sustaining stocks is adequate summer habitat for juveniles.

The mechanism that we have proposed to explain the importance of deep water habitat is the necessity of summer segregation of adult and juvenile lake trout, because of the cannibalistic nature of the species. Cannibalism has been widely observed in lake trout stocks and can represent a very significant mortality factor, even for stocks where the observed incidence of cannibalism is low, as demonstrated here for Lake Opeongo.

Oxygen concentration in deep waters and the amount of deep water were highly correlated with the occurrence of native lake trout and natural production. On average, a lake must be at least 27.5 m deep and have a minimum mean dissolved oxygen content of 2.3 mg L^{-1} oxygen in the deep hypolimnion (27-50 m) to support even a remnant, self-sustaining lake trout population. Any factor that accelerates hypolimnetic oxygen depletion will reduce the quantity and quality of this critically important deep-water juvenile habitat. This nursery habitat is a refugium where juveniles live for several years at temperatures below optimum, but also escape predation by the adults, which live in shallower water. It is possible that juveniles can tolerate lower oxygen concentrations than adults; however, if hypolimnetic oxygen depletion forces the juveniles into shallower water, they become more vulnerable to cannibalism.

Density-dependent size-selective cannibalism appears to be an important natural phenomenon of lake trout populations. Not only could it occur between the adults and juveniles, which would tend to regulate overall population size, but it could also occur among juveniles within the deep-water nursery habitat. This has important management implications, because the size of the nursery habitat appears to control natural recruitment. The entire natural lake trout production of a lake, therefore, is dependent on the quantity and quality of the nursery habitat. If hatchery fish are stocked in the lake, they will also use the nursery habitat and become competitors and possibly predators of the native recruits. If stocking is heavy, predation by adult domestic lake trout on native and domestic juveniles would have a suppressive effect on recruitment.

The deep-water nursery habitat is only a small percentage of the total volume of the lake. This critical volume may be one of the most important factors limiting lake trout production under natural conditions. The abundance of juvenile lake trout and oxygen conditions in deep water would provide important indices for monitoring the status of lake trout populations and for determining the ability of the lake to support a self-sustaining population. Management of lake trout stocks should take into consideration the quality, volumes, and natural abundance and carrying capacities of the various habitats, especially that of the deep-water nursery habitat. This habitat is the depth stratum that is most vulnerable to the effects of nutrient enrichment, because of its greater isolation from the lake surface, and the influence of the benthic sediments on oxygen demand.

Theoretically, habitat degradation can be equated with increased risk of mortality, because of the general suppressive effect on scope for activity (Priede 1977), including such functions as foraging, growth and escape from predators. The exact relationships between habitat losses and mortality are not known, but can be modelled using some simple assumptions. For example, we assumed that certain types of habitat loss can be equated with percentage increases in mortality, and modelled various hypothetical scenarios accordingly (Table 31). The results revealed that habitat related declines in early survival could have dramatic consequences for the adult stock (Fig. 60-64).

Habitat degradation could also influence the scope for activity of the adult stock, and thereby influence population dynamics in more subtle ways through growth effects on maturity, and fecundity. Viability of gametes might also be reduced under the influence of some habitat or environmental stressors, such as direct toxicants or bioaccumulating contaminants. These factors could be modelled, using our population model, by applying the same approach as for degradation of early life habitat, but we have not done so.

GENETIC IMPLICATIONS OF STOCKING

Of the 1474 extant native lake trout stocks in Ontario, 335 have received plantings of hatchery-reared lake trout and 324 of those have been introductions of non-native origin. Thus, 22% of all native stocks have received at least one introduction of non-native lake trout. In only 11 cases have native stocks been used in hatchery plantings in Ontario. The main implication of this approach is the potential for genetic introgression and transformation of the native gene pool. Even in the

absence of reproduction of introduced stocks or hybridization between hatchery and wild lake trout, stocking can lead to the loss of the native gene pool. This occurs when artificial recruitment exceeds natural recruitment and is greatly accelerated at high exploitation rates. If the same or a few hatchery stocks are used to stock native populations, the effect will be to dramatically reduce genetic heterogeneity and, in turn, to reduce the fitness of the affected populations. Widespread stocking of non-native hatchery stocks, therefore, poses a serious risk to the genetic diversity of the species.

We suggest the following directions for the genetic management of native lake trout stocks:

- emphasis should be placed on protection of the remaining self-sustaining lake trout stocks; a moratorium on supplemental stocking of these populations with hatchery-reared lake trout should be considered;
- supplemental stocking should be from native stocks where this practice is deemed necessary;
- if native stocks are not available, the donor stock should be genetically as close as possible to the recipient stock; and
- loss of genetic variability and adaptation to hatchery conditions should be minimized in the donor stock.

Since considerable information on the genetic differentiation of Ontario lake trout is available (Ihssen et al. 1988), and since methods have been developed for better genetic maintenance of hatchery brood stocks (Ryman and Utter 1986), it should be possible to implement these proposed new directions into lake trout management plans.

CONCLUSIONS

- Variation in lake trout harvest among lakes is primarily caused by differences in fishing effort, but other factors, including lake size, lake productivity, habitat quality, and season, also have significant effects.
- Yields of lake trout in many small lakes appear to be well in excess of the capacity of the natural production systems to sustain them. Extensive stocking of hatchery-reared lake trout is serving to maintain high fishing intensities on many lakes, especially during winter, but is also providing high yields in number of fish caught. Yield in biomass for stocked lakes is less than for self-sustaining populations, possibly because fish are being harvested at small body sizes and at rates well in excess of MSY. It is not clear, however, whether yields of stocked lakes are lower because

of inherent lower productivity or excessive exploitation. We speculate that stocked lakes are generally less productive for lake trout and more vulnerable to overfishing and other stressors. Our assessment of nursery habitat for wild and stocked populations supports this interpretation. Stocked lakes, in general, had less and lower quality habitat for lake trout than lakes supporting self-sustaining stocks.

- Angling pressure on lake trout stocks was greatest during winter, winter fishing intensity being about 25% greater than the spring and summer intensity combined. Winter yields exceeded spring and summer yields and were similar to the yields for the entire open-water season, varying from about 1.16 kg ha⁻¹ for 100 ha lakes to about 0.10 kg ha⁻¹ for 10,000 ha lakes. Stocking tends to mask serious overexploitation and, in the absence of stringent harvest controls, is not effective as a rehabilitation technique. In fact, because stocking tends to stimulate exploitation, this approach can cause further degradation of the resource, because locally adapted wild stocks can be displaced by the hatchery stocks.
- Fishing intensity and yields were highest on small lakes, consequently small lakes are most vulnerable to overfishing. Reductions of harvests are required on many lakes of about 1500 ha and less, if self-sustaining wild stocks are to be preserved in these lakes. In general, yields >0.75 kg ha⁻¹yr⁻¹ are considered to be excessive.
- Additional research is required to evaluate variation in lake trout production between lakes, because a single yield guideline (i.e. 0.75 kg ha⁻¹yr⁻¹) is not adequate for all lakes and must be considered only as an interim guideline. Small lakes, in particular, appear to be inherently more productive than larger lakes, and other factors, including morphometry, productivity and habitat quantity and quality, influence lake trout production. Managing all lakes to the same guideline would inevitably lead to the loss of less productive populations and under-utilization of the most productive ones. There is a serious risk of losing some less productive, but possibly uniquely adapted local stocks, due to lack of understanding of their vulnerability to exploitation mortality.
- Use of two rods during winter appears to cause a significant increase in harvest per angler. This effect is greatest in small lakes, because fish densities are greater, fish are distributed more uniformly in the more homogeneous habitats of these waters, and are more easily located by anglers. Also, two lines of one angler "search" a greater portion of the lake area in small lakes.
- Lake area was a useful predictor of relatively unregulated fishing effort, annual effort increasing approximately by area to the power 0.60 during the period 1960-1984. Lake area, however, is not an effective predictor of lake trout harvests unless the lakes being compared are homogeneous

with reference to relative habitat volumes and qualities. Lake trout harvests of inland Ontario lakes varied by 1-2 orders of magnitude (i.e. 10- to 100-fold) for lakes of the same surface area. Maximum sustained yields for five heavily exploited, wild populations (Bone, Chiblow, Christman, Flack, and Opeongo) were strongly correlated with lake area, but these lakes represent high quality lake trout habitats and all have strong natural reproduction. Annual yields, predicted on the basis of area for these five lakes, were 65-161% greater than the predicted mean for all other lakes combined, over the range of 100 to 10,000 ha.

- HUE is inversely related to fishing intensity. Harvest increases with increasing effort until a maximum (MSY) is reached, at which point further increase in effort causes a decline in harvest, therefore, HUE at MSY will be considerably below maximal HUE for a particular lake or set of similar lakes. HUE will vary as a function of fishing intensity on such lakes. Over all lakes of varying productivity, potential HUE will vary as a function of standing stocks of lake trout (i.e. carrying capacity of the lakes). Less productive lakes will have low HUE at low fishing intensity, even at the initial stage of exploitation, and will have a much lower HUE at MSY than more productive lakes. In order to use HUE as a comparative measure of exploitation status, therefore, the production status of a particular lake must be known.
- HUE in number of fish was inversely related to lake area for winter fisheries, indicating higher success rate and possibly higher vulnerability of lake trout to winter fishing in small lakes. In contrast, HUE (kg) was positively related to lake area for open-water and annual fisheries, indicating greater success in large lakes during summer, although HUE (number) was not significantly related to lake area. Given that fishing intensity is much greater in small lakes than large ones during all seasons, these results suggest that small lakes are, in fact, more productive on a per hectare basis than large lakes.
- Summer nursery habitat quantity and quality is a critical factor for natural production of self-sustaining, wild lake trout stocks. Vital lake trout habitat was defined as having temperature $>15.5^{\circ}\text{C}$ and dissolved oxygen concentration $>4\text{ mg L}^{-1}$. During summer stratification, adult lake trout are segregated from the juveniles; both occupy the hypolimnion, but the juveniles are found at greater depths (27-50 m versus 18-28 m) and colder temperatures (juveniles: 2.7-8.6; adults: 2.8-11.1).
- Thresholds for extinction of self-sustaining lake trout stocks correspond to habitable volume (2.5 mg L^{-1} dissolved oxygen to 15.5°C) equal to 35% of total volume; mean oxygen concentration of juvenile depth range (27-50 m) equal to 2.3 mg L^{-1} or 17% saturation; and mean oxygen

concentration of the adult depth range (18-28 m) was 2.6 mg L^{-1} of 20% saturation. Thresholds for the presence of low but persistent native stocks (i.e. N5 status) for the mean juvenile depth range was about 3.7 mg L^{-1} or about 28% saturation, and for the mean adult depth range was 4.0 mg L^{-1} or about 30% saturation.

- Strong, self-sustaining wild stocks of lake trout were found where the mean oxygen concentration of the adult and juvenile depth ranges were about 5.8 mg L^{-1} or 50% saturation, and 6.0 mg L^{-1} or 47% saturation, respectively.
- Nutrient (*P*) additions from cottage and other recreational development or municipal sewage inputs that increase primary productivity and, in turn, increase lake metabolic rates and decrease hypolimnetic oxygen concentrations, will affect lake trout production, especially if dissolved oxygen concentrations reach the incipient response thresholds ($4\text{--}6 \text{ mg L}^{-1}$) for juvenile fish. Once these levels are reached, scope for activity declines and the risk of mortality increases. The lower response threshold for avoidance (4 mg L^{-1}) corresponds closely to the mean oxygen conditions actually observed for marginal self-sustaining stocks (i.e. status N5) noted above.
- Segregation of juvenile and adult lake trout during summer is probably due to cannibalism of the adults, which acts as a density-dependent population regulation mechanism. Cannibalism is suggested as a key factor necessitating a deep water nursery habitat in lakes in the southern part of the species range throughout Ontario.
- Stocking of self-sustaining lake trout populations with hatchery-reared lake trout stimulates angling and tends to maintain high fishing intensities. High stocking rates, needed to sustain the harvests, appear to greatly exceed natural recruitment in these lakes. In these cases, the wild stock is replaced by the hatchery stock, even when the latter does not reproduce or sterile stocks are used. Widespread stocking of non-native hatchery stocks, therefore, poses a serious risk to the genetic diversity of the species. A moratorium is needed on stocking of all remaining self-sustaining wild stocks until such time that a scientifically sound management strategy, including genetic assessment and productive capacities, has been completed for the provincial lake trout resource.
- Population modelling revealed the sensitivity of lake trout populations to exploitation and changes in early survival. Fishing mortality in excess of $F = 0.4\text{--}0.6$ for Lake Opeongo, for example, was at the limit of the natural compensatory recruitment capacity for that population. Lakes having lower productivities or less pristine habitats would have lesser capacity to respond to fishing, yet fishing mortalities of $F = 0.4\text{--}0.6$ appear to be in the low to mid region of the observed range for Ontario lake trout stocks.

- Total annual mortality associated with MSY for very productive lake trout stocks was roughly estimated to be about 0.5 ($Z = 0.69$). Critical instantaneous fishing mortality rates, corresponding to MSY for less productive or stressed lake trout stocks, would be expected to vary from zero to 0.59, assuming instantaneous natural mortality to have a value of at least 0.10. This implies that some weakly recruiting lake trout stocks might not be capable of sustaining any fishing mortality. Further research is required to better understand the relationships between productive capacity, lake characteristics, and surplus production that can be harvested without depreciation or loss of lake trout stocks. Payne et al. (1990) suggested 0.45-0.50 as a safe upper limit for total annual mortality.
- The major influence of early mortality on lake trout population dynamics, revealed by our population model, suggests that degradation or loss of early life habitats would have significant effects on production of lake trout. Degradation of early life habitats, including spawning habitat and especially the critical summer nursery habitat, must be prevented if production levels of self-sustaining wild stocks are to be maintained.
- Population modelling revealed the need for major regulatory commitments because of the lengthy time frames required for rehabilitation of overexploited stocks and degraded environments, even under the most optimistic circumstances where stock depletion is directly reversible.
- A major review of present lake trout stocking practices is required to establish a coordinated approach to managing the provincial resource. New knowledge about exploitation, habitat requirements, and stocking effects need to be incorporated into a unified strategy that will prevent further erosion of the resource. Improved inventory of lake trout stocks and lakes is required for management decision making to ensure continuation of a genetically diverse and productive self-sustaining resource. The focus needs to be placed on wild self-sustaining stocks to ensure viable populations and retention of the genetic diversity and vitality of the resource. Some lakes, where native stocks have been lost and prospects for rehabilitation of wild stocks are low, might continue to be managed using hatchery stocks. Where hatchery stocks are required, native or well matched stocks should be employed to minimize genetic impacts. These decisions should not be taken, however, without critical scientific input.

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Appendix A. Geographical information for lake trout lakes for which creel survey information is analyzed herein.

Lake no.	Lake name	Township	Region	District	Water-shed	Latitude (°N)	Longitude (°W)	Elevation (m)
1	Anstruther	Anstruther	AL	52	210808	4445	7812	313
2	Ayles	Dickens	AL	51	2K009	4537	7751	335
3	Bapineau	Herschel	AL	52	2K002	4507	7803	352
4	Bark	Jones	AL	56	2K001	4527	7751	313
5	Basswood	Day	NE	41	2CC08	4619	8324	211
6	Bay	Faraday	AL	52	2K005	4501	7752	354
7	Bella	Sinclair	AL	53	2EB15	4526	7802	356
8	Bernard	Strong	AL	53	2EA20	4545	7923	330
9	Best	Brigsteche	NE	46	2JE13	4715	7950	326
10	Big Clear	Bedford	E	64	2MA06	4433	7628	-
11	Big Hawk	Stanhope	AL	54	21F08	4510	7844	360
12	Big Porcupine	Lawrence	AL	51	2EB11	4527	7837	408
13	Big Ribbon	N & S Burgess	E	61	2LA07	4445	7613	124
14	Big Salmon	Bedford	E	64	2MA06	4432	7630	-
15	Blue	McAuslan	NE	43	2JE12	4644	7919	336
16	Bone	Tipper	NE	44	2BF03	4648	8416	305
17	Bonnechere	Lawrence	AL	51	2K001	4528	7835	441
18	Boothby	Stanhope	AL	54	21F08	4504	7844	308
19	Back Lake (McCann)	Proudfoot	AL	53	2EB22	4541	7910	423
20	Cassels	Cassels	NE	46	2JE13	4704	7943	296
21	Chandon	Chandon	AL	52	21K07	4449	7800	312
22	Charleston	Road of Leeds	E	61	2MA09	4432	7600	86
23	Chilhow	Scarle	NE	41	2CD06	4621	8303	233
24	Christmas	Rainbow	NE	41	2CC06	4635	8244	360
25	Clearwater	Armagh	NE	46	2DC06	4702	8018	313
26	Cradle	Lawrence	AL	51	2K001	4528	7835	441
27	Cucumber	MacBeth	NE	43	2DC01	4630	8019	287
28	Cut	McAuslan	NE	43	2JE01	4646	7916	320
29	Dana	Dana	NE	43	2DC01	4643	8016	285
30	Devil	Bedford	E	64	2MA06	4435	7627	131
31	Dickey	Lake	E	66	21K10	4447	7744	320
32	Dickson	Dickson	AL	51	2K012	4547	7812	386
33	Drag	Dudley	AL	54	21F09	4505	7824	354
34	Eagle Rock		NE	43	2DC06	4635	8015	-
35	Elia	Anstruther	AL	52	210807	4454	7808	366
36	Elliot	Boiger	NE	41	2CD07	4623	8242	305
37	Emerald	Afton	NE	43	2DC01	4654	8019	315
38	Elson (Omer)	Dudley	AL	54	21F05	4501	7816	405
39	Faraday (Trout)	Faraday	AL	52	2K002	4504	7755	361
40	Flack	Rainbow	NE	41	2CC06	4635	8247	353
41	Gong	Handelman	NE	44	2CB02	4705	8332	450
42	Goulds	Butcher	NE	44	2BF03	4710	8340	480
43	Gull	Latterworth	AL	54	21F07	4451	7847	270

Appendix A. Continued.

Lake no.	Lake name	Township	Region	District	Water-shed	Latitude (°N)	Longitude (°W)	Elevation (m)
44	Gull	Scholes	NE	46	2DC06	4654	8012	322
45	Haliburton	Halburn	AL	54	2H010	4512	7824	361
46	Halt	Stanhope	AL	54	2H008	4506	7845	326
47	Iron	Mercedish	NE	44	2CA03	4630	8356	267
48	Joseph	Madura	AL	53	2EB05	4511	7947	225
49	Jumping Caribou	Law	NE	46	2DC06	4653	7947	302
50	Kashagewiganog	Minden	AL	54	2H009	4459	7836	316
51	Kawagoma	Sharburne	AL	53	2EB12	4518	7845	335
52	Kennan	Hawcock	AL	54	2H008	4513	7858	369
53	Kimball	Livingstone	AL	53	2EB12	4521	7841	358
54	Kochling	Olamorgan	AL	54	2H006	4458	7829	347
55	L'Amable	Farnley	AL	52	2KD05	4501	7749	312
56	Lake of Bays	Sharburne	AL	53	2EB10	4515	7834	316
57	Lake of the Woods ¹	21 Townships	NW	14	SPD	6930	9420	-
58	Lake of the Woods ²	21 Townships	NW	14	SPD	6930	9420	-
59	Lake St. Peter	McClure	AL	52	2KD12	4519	7802	399
60	Larder	Hesse	N	36	2/C94	4805	7958	282
61	Lawville	Anglin	AL	51	2KB12	4551	7854	586
62	Limerick (Bear)	Limerick	AL	52	2H009	4453	7757	313
63	Long (Elephant)	Proudfoot	AL	53	2EA22	4542	7911	381
64	Loon	Simcoe	AL	53	2EB15	4523	7859	586
65	Louisa	Lawrence	AL	51	2KD19	4528	7829	441
66	Lower Bass	Bathurst	NE	46	2DC08	4659	8015	358
67	Manitou	Sandfield	NE	42	2CC09	4545	8038	-
68	Manitou (Devil)	Chenest	NE	43	2DC01	4651	8017	266
69	McConnell	McAuliffe	NE	43	2JE12	4644	7921	316
70	Magnan	Cochran	NE	44	2CB02	4715	8352	442
71	Murphree (Devil)	Cochet	AL	52	2H009	4456	7755	312
72	Muskoka	Dudley	AL	54	2H008	4505	7819	393
73	Mississauga	Cavendish	AL	54	2H008	4442	7819	295
74	Moncton	Minden	AL	54	2H008	4459	7841	336
75	Muskoka	Muskoka	AL	53	2H004	4500	7823	225
76	Nat	Steele	NE	46	2JE15	4706	7946	296
77	Nauyas (Crab)	Sharburne	AL	54	2H008	4512	7844	377
78	Oyungo	Bower	AL	51	2KD10	4542	7823	404
79	Papineau	Wicklow	AL	52	2KD11	4521	7749	317
80	Percy (Pine)	Halburn	AL	54	2H010	4512	7822	361
81	Percy (Loon)	Proudfoot	AL	53	2EA22	4540	7913	412
82	Pond	Afion	NE	43	2DC01	4657	8019	317
83	Rabin	Riddell	NE	46	2JE15	4700	7958	290
84	Ranger	Reilly	NE	44	2CA02	4654	8334	439
85	Rushmore	Quilford	AL	54	2H011	4511	7832	364
86	Russell	Madura	AL	53	2EB05	4510	7935	225
87	Seminar	Hendrick	NE	41	2CC06	4655	8241	366

Appendix A. Continued.

Lake no.	Lake name	Township	Region	District	Water-shed	Latitude ("N)	Longitude ("W)	Elevation (m)
88	Sherborne (Trout)	Sherborne	AL	54	2HFB8	4511	7847	358
89	Silent (Pine)	Cardiff	AL	52	2HKG7	4455	7804	359
90	Simcoe		C	74	2HC	4425	7800	
91	Skeleton	Watt	AL	53	2HBO7	4515	7927	281
92	Smoke	Peck	AL	51	2HBI1	4531	7841	422
93	Spring	McAmian	NE	43	2HBI1	4646	7917	320
94	Temagami	11 Townships	NE	46	DCU26	4700	8005	294
95	Thonet	Lake	E	66	2HK11	4447	7746	305
96	Timberwolf	Hunter	AL	51	2KB13	4541	7848	427
97	Trout	Widdifield	NE	43	2HE02	4618	7920	214
98	Turtleshell	Scholes	NE	43	2DCD1	4653	8015	297
99	Twelvemile	Minden	AL	54	2HFB8	4501	7843	308
100	Wawigama	Armagh	NE	46	2DCU8	4659	8024	282
101	Wawinshkashi	McNish	NE	43	2DCD1	4648	8020	265
102	White Partridge	Niven	AL	51	2KB04	4550	7806	352
103	Wollaston	Wollaston	AL	52	2HK11	4451	7750	307
104	Yurston	Seagram	NE	45	2DCU9	4703	8032	327

¹Whitefish bay²Clearwater bay

Appendix B. Selected physical-chemical characteristics for lake trout lakes for which creel survey data are analysed.

Lake no.	Lake name	Surface area (ha)	Mean depth (m)	Maximum depth (m)	Seuchi (m)	pH	TDG (mg L ⁻¹)	TP (mg L ⁻¹)
1	Amstruther	633.8	12.6	39	4	-	-	-
2	Ayles	2016.8	27.2	72.9	6.7	7.0	35	0.0050
3	Baptiste	2226.3	4.7	52	4.3	8.5	40.09	-
4	Bark	3801	24.3	87.5	4.6	7.0	31	0.0040
5	Basswood	2708	-	-	-	-	-	0.0040
6	Bay	84.9	10.8	21.9	10.4	8.5	151.36	-
7	Bella	337.8	16.2	40	6.1	6.4	25.91	-
8	Bernard	2185.3	15.1	47.9	3.7	7.0	38.63	0.0080
9	Bent	84	5.7	30.8	5.3	7.5	41.63	-
10	Big Clear	187.4	20.1	61	8.4	-	50	-
11	Big Hawk	388.5	-	-	-	6.5	-	-
12	Big Porcupine	235.3	7.5	31.7	7.6	7.0	45.42	0.0047
13	Big Redden	575.1	13.3	100	4.9	9.0	138	-
14	Big Salmon	148.1	13.2	42.4	8	-	58	-
15	Blair	177	6.7	25.6	10.8	7.0	26.97	-
16	Bone	123.1	7.7	32.6	5.5	6.6	29.97	-
17	Bonnechere	104.5	6.4	22	6.7	7.0	22.71	0.0052
18	Bonhous	715.9	23.1	71.1	6.1	7.5	34.7	-
19	Buck (McCann)	87.1	13.6	45.8	9.8	6.4	19.51	-
20	Cassidy	772	9.6	36.6	-	7.2	57.94	-
21	Chandon	1367.4	13.3	47.0	5.5	8.0	133.2	-
22	Charleston	2550.2	17.4	91.1	4.6	9.0	137	-
23	Chisholm	2388.7	23.9	70.2	7.8	-	-	0.0050
24	Christmas	57.9	7	18.3	6.3	7.5	46.02	-
25	Clearwater	111.6	13.8	47	10.7	7.0	33.3	0.0070
26	Cradle	16.8	11.2	33.6	4.9	7.0	26.51	0.0059
27	Cucumber	80.6	10.3	22.9	5	7.5	40.95	-
28	Cut	70.4	13	39.7	9.8	7.5	87.38	-
29	Dana	110.5	7.4	25.9	2.7	6.5	29.77	-
30	Devil	1061.3	14.4	44.5	5.5	8.0	109	-
31	Dickey	214	18.3	54	5.1	8.5	90	0.0037
32	Dickson	975	5.5	16.8	4.2	7.0	33.3	-
33	Drag	1002.8	17.8	55	5.3	7.5	38.7	0.0030
34	Eaglehawk	167.6	13.1	42.7	6.7	-	13.99	-
35	Fish	945.8	6.7	29.9	5.8	7.0	26.14	-
36	Elliot	616	15.5	36.1	5.1	6.3	69.3	-
37	Emerald	566.8	18.5	48	6.4	7.0	55.5	0.0010
38	Falcon (Oster)	250.6	10.8	32	6.5	8.5	70.86	-
39	Faraday (Trout)	114	9.1	24.4	5.6	7.0	58.28	-
40	Flick	951	19.9	70	11.2	7.1	22.3	0.0040
41	Gong	385	6.9	21.3	4	7.0	24	0.0110
42	Goulden	240	9.1	33.5	3.6	-	31.4	-
43	Gull	995.1	16.5	49.1	5.8	7.0	41.82	-

Appendix B. Continued.

Lake no.	Lake name	Surface area (ha)	Mean depth (m)	Maximum depth (m)	Secchi (m)	pH	TD5 (mg L ⁻¹)	TP (mg L ⁻¹)
44	Gull	1312.2	20.3	54.0	6.4	7.0	29.57	0.0050
45	Haliburton	997.6	-	-	-	7.0	-	-
46	Halls	539.8	-	-	-	7.3	-	-
47	Iron	217.9	10.9	45.7	4.7	6.8	24.78	-
48	Joseph	4972.8	24.7	93	6	7.0	45	-
49	Jumping Caribou	408.7	8.9	33.6	5	7.5	33.15	0.0050
50	Kashagwigamog	778.4	-	-	-	7.5	-	-
51	Kawagama (Hollow)	2818.6	21.8	73.2	11.0	7.5	22.18	-
52	Kennison	1360.1	23.3	66	9.3	6.5	23.3	0.0020
53	Kimball	212.5	22.8	67.1	9.1	7.0	25.31	0.0037
54	Koshkong	489	10.2	42	5.2	6.5	22	0.0010
55	L'Amable	178.4	23	35	5.7	9.0	83.25	-
56	Lake of Bays	7052.0	22.2	70.1	6.3	6.8	23.32	-
57	Lake of the Woods ¹	20655	7.9	68.8	7.2	-	137.9	-
58	Lake of the Woods ²	3000	7.9	68.8	7.2	-	137.9	-
59	Lake St. Peter	231.3	7.9	28	3.5	-	-	-
60	Larder	3670	12.3	33.5	4.3	7.8	127.07	-
61	Lavoie	2402	14.4	48.8	5.1	7.0	31.6	-
62	Limerick (Basin)	828.8	9.7	30	4.6	9.0	140.19	-
63	Long (Elephant)	175.6	13.9	33.5	7	8.0	-	-
64	Loon	155.4	9.2	15.1	6.6	8.5	22.1	-
65	Lowie	531	17	61	6	6.5	22.5	0.0050
66	Lower Basin	105.3	8	21.4	7	6.5	36.83	-
67	Manitou	10804	15.1	49.1	8.4	-	180.5	-
68	Manitou (Devil)	322.3	18	47.6	8.4	7.1	41.89	-
69	McConnell	207.2	12.1	32.9	5.2	7.0	25.17	0.0080
70	Meghan	628	5.8	18	3.6	7.0	34	0.0110
71	Mephitis (Devil)	166.6	14.7	42	6.8	9.0	149.85	-
72	Miskwabi (Misquabishish)	267.9	19.1	44.2	7.9	7.0	61.87	-
73	Missisquoi	587.6	-	-	-	6.5	-	-
74	Mountain	319.3	-	-	-	8.0	-	-
75	Muskoka	10521.8	15	66.5	3.1	7.0	60.5	-
76	Nat	711	7.8	47.5	5.5	6.0	51.35	-
77	Nunikani (Crab)	115.6	7.9	24.1	7.2	6.5	20.25	0.0045
78	Opeongo	5860	14.6	49.4	5.8	7.0	29	-
79	Papineau	830.8	19.4	61	8.5	-	-	-
80	Percy (Pine)	341	-	-	-	7.5	-	-
81	Peversey (Loon)	155.4	9	26.2	6.9	6.8	21.71	-
82	Pond	21.5	11.5	23.5	9.8	7.0	21.25	-
83	Rabbit	2083	14.2	42.7	5.8	7.5	63.07	0.0040
84	Ranger	2255.1	21.7	73.2	8.7	7.5	25.31	-
85	Redstone	1130.3	21.9	82.4	6.1	6.7	64	-
86	Roscoe	5827.5	23.2	90	1.5	7.0	33.4	-
87	Semiwa	304.5	12.4	33.5	7.6	6.8	27.97	-

Appendix B. Continued

Lake no.	Lake name	Surface area (ha)	Mean depth (m)	Maximum depth (m)	Secchi (m)	pH	TDS (mg L ⁻¹)	TP (mg L ⁻¹)
88	Sherburne (Trout)	251.8	9.5	35.1	9.2	6.5	23.71	0.0046
89	Silent (Pine)	137.5	6.5	23.1	5.4	7.0	29.3	.
90	Simcoe	72500	17	41.5	5	8.3	199.8	.
91	Skelton	2155.4	28.9	64.7	9.2	6.7	29.57	0.0050
92	Smoke	607	16.2	54.9	5.7	8.0	25	0.0090
93	Spring	69.6	22.3	54.9	15.3	7.8	70	.
94	Temagami	21327.2	18.2	110	10.7	7.0	48.4	0.0040
95	Thonet	109.2	8.7	26.8	5.9	8.5	70.86	.
96	Timberwolf	167.8	7	20.4	3	7.0	21.6	0.0065
97	Trout	1041	16.9	69.2	3.8	6.5	46.82	.
98	Turtleshell	161.1	12.5	45.9	7	.	30	.
99	Twelvemile	336.7	10.6	24	5.2	7.0	34	0.0010
100	Wawigama	576.8	8.8	20.4	3.8	8.5	59.21	.
101	Wawinshukashi	414.1	5.6	21.4	4.6	7.0	53.75	.
102	White Partridge	575	15.2	47.3	5.9	8.0	34	.
103	Wollaston	363	9.4	31.1	4.6	8.0	161.84	.
104	Yveston	355.8	11	45	8.5	6.5	29.9	0.0040

^aWhitfish Bay^bClearwater Bay

Appendix C. Development, introduction and stocking information for lake trout lakes for which creel survey data are analyzed herein.

Lake no.	Lake name	Stock status ^a	Dam	Water level ^b (m)	Acres ^c	No. of cottages	No. of cottages	No. of lodges	No. of fishing guides ^d	Species introductions ^e	No. of lake trout stocked ^f	No. of years stocked ^g
1	Amstrutler	N3	Y	1.4	01	214	-5	3	0	070 316 317	4750	4
2	Aylen	N1	Y	-	01	270	25	1	0	316	10000	2
3	Bayshore	O	Y	1.0	11	400	>100	17	0	080 093 132 311 316 317 334	-	0
4	Bark	N3	Y	10	05	50	0	0	0	093 121 316	15000	6
5	Barnwood	N1	Y	-	11	200	20	3	1	121	-	0
6	Bay	N3	N	-	11	50	>50	1	0	076 311 316	2613	4
7	Bella	N3	-	-	-	-	-	-	-	-	280	3
8	Bernard	N3	-	-	-	-	-	-	-	-	1100	3
9	Bess	N3	N	-	M	0	0	0	0	No	1039	3
10	Big Clear	N3	N	-	11	<14	<14	0	0	076 077 082 317	1367	6
11	Big Hawk	N3	Y	2	01	150	00	1	0	Unknown	6033	3
12	Big Porcupine	N1	N	-	L	0	0	0	0	Unknown	-	0
13	Big Salmon	N3	Y	-	11	>500	>500	8	0	061 076 077 132 317	18000	3
14	Big Salmon	N3	N	-	11	0	0	0	0	082 317	1000	2
15	Blair	02	N	-	01	0	0	0	0	082	1007	3
16	Bloom	N1	N	-	04	3	0	0	0	No	-	0
17	Bonnetville	N1	N	-	L	0	0	0	0	Unknown	-	0
18	Bonkburg	N3	Y	0.0	01	2	<200	4	3	121 311 316 317	4013	1
19	Buck (McConn)	11	-	-	-	-	-	-	-	-	2232	3
20	Cassidy	N3	Y	4.5	01	25	0	0	0	No	4323	3
21	Chandon	N3	N	-	11	080	>100	0	0	093 131 311 316 317 334	9733	3
22	Charleston	N3	Y	-	01	<080	<080	20	0	076 077 078 317	17000	7
23	Chickadee	N1	Y	-	11	15	2	1	0	121	-	0
24	Christmas	N1	-	-	-	-	-	-	-	-	-	0
25	Clearwater	N1	N	-	11	0	0	0	0	No	-	0
26	Cradle	N1	N	-	L	0	0	0	0	Unknown	-	0
27	Cucumber	N3	N	-	11	1	0	0	0	No	1500	3
28	Cut	11	N	-	11	0	0	0	0	No	1351	4
29	Dana	N3	N	-	01	1	0	0	0	No	-	0
30	Devo	N3	Y	1.5	01	<225	<225	51	1	317 334	5000	7
31	Dickey	N3	N	-	01	>45	>45	0	0	093 311 316 317	1676	6
32	Dickson	N1	N	-	L	0	0	0	0	No	-	0
33	Doug	N1	Y	1.09	11	0	0	0	0	076 078 093 311 313 316 317 331	4500	2
34	Englewick	N3	N	-	11	0	0	0	0	No	-	0
35	Erie	O	Y	2.4	01	567	<10	2	0	080 311 316 317 334	5700	1
36	Eller	N1	Y	-	11	0	0	0	0	121 233 311 313 316	-	0
37	Emerald	N1	N	-	11	41	0	2	0	080	-	0
38	Faxon (Oster)	N3	-	-	-	-	-	-	-	-	1750	2
39	Faraday (Trout)	N3	N	-	01	06	<25	1	0	076 080	2250	2
40	Flack	N1	Y	-	11	0	0	0	0	311	-	0
41	Gong	N3	N	-	11	0	0	2	0	No	-	0
42	Goulden	N1	N	-	01	0	0	1	0	No	-	0
43	Gull	N1	Y	1	01	410	<600	3	0	121 311 313 316 317	0	0
44	Gull	N3	Y	-	M	4	0	0	0	No	4875	4
45	Hallburton	N3	-	-	-	-	-	-	-	-	4333	3
46	Hall	N3	-	-	-	-	-	-	-	-	4167	3
47	Iron	N3	N	-	11	6	0	0	0	331 316 121	-	0

Appendix C. Continued

Lake no.	Lake name	Stock status ^a	Dam	Water level ^b (ft)	Acres ^c	No. of cottages	No. of residences	Lodges	No. of fishing guides ^d	Species introductions ^e	No. of lake trout stocked ^f	No. of young stocked ^g
48	Joseph	N1	N	-	11	1025	U	12	0	076 121 131 311 317	-	0
49	Jumping Cotton	N1	-	-	-	-	-	-	-	-	-	0
50	Kachagungungung	N3	-	-	-	-	-	-	-	-	-	0
51	Kawaguma (Hobbs)	N1	Y	2.2	11	433	U	3	2	121 316	5500	2
52	Kenneth	O	-	-	-	-	-	-	-	-	-	0
53	Kimball	N1	N	-	11	14	0	0	0	121 311	2075	4
54	Konkang	12	Y	1.4	11	>200	<100	2	0	081 121 316	-	0
55	L'Amable	N3	Y	0.3	11	10	<10	0	0	311	17325	4
56	Lake of Hope	N3	Y	-	11	1576	U	17	0	076 121 316	4450	4
57	Lake of the Woods ¹	N1	Y	1-2	11	>500	400	25	10	011 075 076 080 234 311	3900	4
58	Lake of the Woods ²	N1	-	-	-	-	-	-	-	-	-	0
59	Lake St. Peter	N3	N	-	11	183	<25	10	0	076 080 085 311	3000	1
60	Larder	N3	Y	-	11	5	>200	1	0	081 233 314	6000	3
61	Lavender	N1	Y	-	11	0	0	0	0	No	-	0
62	Limerick (Bass)	N3	N	-	11	118	U	1	0	076 077 081 311 316 317 334	7175	4
63	Long (Clapham)	N1	-	-	-	-	-	-	-	-	-	1
64	Long	N3	-	-	-	-	-	-	-	-	-	0
65	Long	N1	N	-	11	0	0	0	0	No	-	0
66	Long Run	N1	N	-	11	0	0	0	0	No	-	0
67	Manitou	N3	Y	-	11	<450	<450	19	<5	No	-	0
68	Manitou (Dead)	N3	N	-	11	19	0	3	0	081	54172	7
69	McConnell	12	N	-	11	5	0	0	0	076 080 334	4350	7
70	McKenzie	N1	N	-	11	0	0	1	0	No	3470	3
71	McKenzie (Dead)	N3	N	-	11	20	0	0	0	080 311 316	-	0
72	McKenzie	N3	-	-	-	-	-	-	-	-	-	2
73	McKenzie	N3	-	-	-	-	-	-	-	-	-	3
74	McKenzie	N3	Y	-	11	225	>50	4	1	121 311 316 317	3750	2
75	McKenzie	N3	Y	-	11	1018	U	17	0	076 121 131 311 313 316 317	2032	2
76	Net	N1	Y	1.0	11	12	100	1	0	No	4091	4
77	Nordham (Crab)	N3	-	-	-	-	-	-	-	-	-	0
78	Oswego	N1	Y	<1	11	0	0	0	1	081 316	2250	2
79	Papineau	N3	N	-	11	260	<10	4	0	080 081 082	-	0
80	Perry (Fox)	O	-	-	-	-	-	-	-	-	-	3
81	Perryway (Lion)	N3	-	-	-	-	-	-	-	-	-	3
82	Pond	N3	N	-	11	0	0	0	0	080 082	4004	2
83	Rainey	N1	Y	4.5	11	30	0	1	0	No	300	3
84	Ranger	N1	Y	1	11	100	0	1	0	No	-	0
85	Randolph	N1	-	-	-	-	-	-	-	-	-	1
86	Randolph	N3	Y	<1	11	1150	0	10	0	076 121 131 132 311 313	2547	3
87	Randolph	N1	-	-	-	-	-	-	-	-	-	0
88	Randolph	N3	Y	0.9-1.5	11	1	0	0	0	No	3000	2
89	St. John (Fox)	N3	N	-	11	0	0	0	0	080 316 316	1500	4
90	St. John	N3	N	-	11	>500	>500	17	>50	076 121 131 136	65215	7
91	St. John	N3	-	-	-	-	-	-	-	-	-	3
92	St. John	N1	Y	1.5	11	60	0	0	0	081 316	-	0
93	Spring	O	N	-	11	0	0	0	0	076 081 082	2250	2

Appendix C. Continued

Lake no.	Lake name	Stock status ^a	Dam	Water level ^b (m)	Access ^c	No. of cottages	No. of residences	Lodges	No. of fishing guides ^d	Species introductions ^e	No. of lake trout stocked ^f	No. of years stocked ^g
94	Ternagami	N1	Y	1.0	H	750	50	14	0	No	-	0
95	Thelon	N3	N	-	M	4	0	0	0	Unknown	2349	3
96	Timberwolf	N1	N	-	L	0	0	0	0	No	-	0
97	Trout	N3	N	-	M	500	500	0	0	080 (walleye)	9413	7
98	Turkishhat	N3	N	-	H	2	0	0	0	No	3000	1
99	Tussocks	N3	V	1	H	230+	<50	0	1	076 080 121 316 317	4000	3
100	Wanagami	N1	N	-	H	1	0	0	0	No	-	0
101	Wawikshadi	N3	N	-	H	2	0	2	0	334	3750	1
102	White Falls	N2	N	-	L	0	0	0	0	No	-	0
103	Widowon	N3	V	0.0	H	194	<10	0	0	076 080 311 316 317 334	6600	4
104	Yorston	N1	-	-	-	-	-	-	-	-	-	0

^aStatus: N1 = Native population: self-sustaining, unstocked

N2 = Native population: natural reproduction, partly self-sustaining, supplemented by planting of native stock

N3 = Native population: natural reproduction, partly self-sustaining, supplemented by plantings of non-native stock

N4 = Native population: little or no reproduction, population maintained by plantings of native stock

N5 = Native population: little or no reproduction, population maintained by plantings of non-native stock

0 = Other

I1 = Introduced population: no native stock, self-sustaining

I2 = Introduced population: no native stock, population maintained by plantings

^bWater level fluctuates.

^cScale for access: H = high; M = medium; and L = low.

^dNumber of fish guides per lake.

^eSpecies codes from Manual of Instructions, Aquatic Habitat Surveys by D. F. Dodge et al. 1984, Fisheries Branch, Ont. Min. Nat. Resour., Toronto, Ontario.

^fNumber of lake trout stocked per year averaged over total number of years stocked.

^gNumber of years stocked since 1980.

^hWhiskey Bay

ⁱClearwater Bay

Appendix D. Residuals of within season $\log_{10}$ harvest versus $\log_{10}$ effort regressions for individual lakes, based on regressions in Tables 3-7.

Lake name	Effort in	Winter				Spring		Summer		Open water	
		(No.d ⁻¹)		(kg.d ⁻¹)		(No.d ⁻¹)		(kg.d ⁻¹)		(No.d ⁻¹)	
		Ang.hrs	Rod.hrs	Ang.hrs	Rod.hrs	(No.d ⁻¹)	(kg.d ⁻¹)	(No.d ⁻¹)	(kg.d ⁻¹)	(No.d ⁻¹)	(kg.d ⁻¹)
Anstruther		-0.29	-0.39	-0.33	-0.47	0.10	0.23	0.32	0.44	0.24	0.20
Ayles		-0.26	-0.44	-0.12	-0.25	-	-	-	-	0.59	-
Baptiste		-	-	-	-	-	-	-	-	-1.10	-0.75
Bark		-	-	-	-	-	-	-	-	0.49	-
Bay		-	-	-	-	0.01	0.26	-	-	-	-
Bella		-	-	0.32	-	-	-	-	-	-	-0.43
Bernard		-	-	0.33	-	-	-	-	-	-	0.35
Big Clear		0.46	0.15	-	-	-	-	-0.14	-	-	-
Big Hawk		-	-	-	-	-	-	-	-	0.53	-
Big Porcupine		-	-	-	-	-0.13	-0.34	0.61	0.40	0.41	0.33
Big Rideau		0.19	0.12	-	0.33	-	-	0.18	-	-	-
Big Salmon		0.37	0.16	-	-	-	-	-0.05	-	-	-
Bonnechere		-	-	-	-	0.12	-0.13	-	-	-	-
Bushkung		-	-	-0.14	-	-	-	-	-	-	-0.25
Beck (McCaen)		0.29	0.16	-	-	-	-	-	-	-	-
Cassels		-	-	-	-	-	-	-0.09	0.16	-	-
Chandon		-0.11	-0.22	-0.21	-0.37	-0.67	-0.73	-0.69	-0.67	-0.71	-0.67
Charleston		0.36	0.35	-	-	-	-	0.07	-	-	-
Chilow		-	-	-	-	0.26	0.54	-	-	0.26	0.26
Cradle		-	-	-	-	0.65	0.76	-	-	-	-
Devil		0.09	-0.22	-	-	-	-	0.09	-	-	-
Dickey		0.09	0.05	-0.13	-0.22	0.17	0.00	0.16	-0.02	0.09	-0.12
Dickson		-	-	-	-	-0.46	-	-	-	-	-
Drug		0.39	0.39	-0.06	-0.13	-0.22	-0.06	-0.07	-0.03	-0.20	-0.25
Eels		-	-	-	-	0.02	0.21	-0.35	0.17	-	-
Elliott		-0.26	-0.33	-	-	-	-	-	-	-0.02	-
Eason (Otter)		-0.20	-0.16	0.01	-0.05	-	-	-	-	-	0.10
Forsday (Trout)		-0.56	-0.63	-0.57	-0.66	-	-	-	-	-	-
Flack		-	-	-	-	-	-	-	-	0.30	-
Gong		-	-	-	-	-	-	-	-	-0.24	-0.21
Goulais		-	-	-	-	0.29	-	-	-	0.22	-
Gull N = 43		-	-	0.06	-	-	-	-	-	-	-0.34
Haliburton		-	-	-	-	-	-	-	-	-	-0.07
Halls		-	-	-0.31	-	-	-	-	-	-	-0.58
Joseph		-	0.16	0.31	0.26	-	-	-	-	-	0.32
Kashagewigamog		-	-	-0.63	-	-	-	-	-	-	-0.20
Kawagama		-	-	0.05	-	-	-	-	-	-	-0.00
Kennish		-	-	0.20	-	-	-	-	-	-	0.06
Kimball		0.47	0.41	0.65	0.55	0.06	0.30	0.06	-0.24	0.10	0.01
Koshkung		0.01	-0.02	0.19	0.12	-0.27	0.24	-0.16	0.44	-0.33	0.16
L'Amable		-	-	-	-	-0.26	-0.09	-	-	-	-
Lake of Bays		-	-	-0.21	-	-	-	-	-	-	0.11

Appendix D. (Continued)

Lake name	Effort in	Winter				Spring		Summer		Open water	
		(No.d ⁻¹)		(kg.d ⁻¹)		(No.d ⁻¹)		(kg.d ⁻¹)		(No.d ⁻¹)	
		Ang.hrs	Rod.hrs	Ang.hrs	Rod.hrs	(No.d ⁻¹)	(kg.d ⁻¹)	(No.d ⁻¹)	(kg.d ⁻¹)	(No.d ⁻¹)	(kg.d ⁻¹)
Lake of the Woods(1)	0.25	-	0.01	-	-	-	-	-	-	-	-
Lake of the Woods(2)	0.33	-	-0.05	-	-	-	-	-	-	-	-
Laville	-	-	-	-	-	0.22	-	-	-	0.19	-
Long (Oliphant)	-0.22	-0.32	-	-	-	-	-	0.16	-	-	-
Loon	-0.10	-0.22	0.22	0.06	-	-	-	-	-	-	-
Manitou	-	-	-	-	-	-	-	-	-	0.16	0.20
Meghan	-	-	-	-	-	0.23	-	-	-	0.20	-
Miskewi	0.06	0.16	0.18	0.06	-	-	-	-	-	-	0.25
Minisagau	-	-	0.23	-	-	-	-	-	-	-	-0.37
Mountain	-	-	-0.69	-	-	-	-	-	-	-	-
Muskegon	-	-0.36	-0.07	0.15	-	-	-	-	-	-	0.28
Nanikani (Crab)	-0.26	-0.14	-	-	-	0.28	0.31	0.29	-0.01	0.23	0.15
Opeongo	-	-	-	-	-	-	-	-	-	0.19	-
Perry (Pine)	-	-	-	-	-	-	-	-	-	-	0.02
Pevensey (Loon)	-	-	-0.29	-	-	-	-	-	-	-	-0.21
Ranger	0.32	-	0.14	-	-	-	-	-	-	-	-
Redstone	-0.34	0.13	0.38	0.48	0.18	0.38	-	-	-	-0.63	0.20
Rosseau	-	-0.12	0.01	0.30	-	-	-	-	-	-	0.23
Sherborne	-0.07	-0.09	0.06	-0.01	-0.05	0.09	0.07	-0.09	-0.09	0.03	0.02
Silent (Pine)	-0.10	-0.22	-0.36	-0.51	-0.09	-0.03	-0.06	0.10	-0.11	0.06	-
Simcoe	-0.29	-0.20	-	-	-	-	-	-	-	-	-
Skatecon	-	-	0.09	-	-	-	-	-	-	-	0.10
Smoke	-	-	-	-	-0.00	-	-0.05	-	-	0.02	-
Temagami	-0.01	-	0.13	-	-	-	-	-	-	-0.04	-0.23
Thornet	-0.73	-0.82	-0.56	-0.67	-	-	-	-	-	-	-
Timberwolf	-	-	-	-	0.37	-	-	-	-	-	-
Twilhemile	-0.36	-0.11	-0.17	-0.20	-0.46	-0.49	-0.41	-0.32	-0.39	-0.16	-
White Partridge	-	-	-	-	0.10	-	-	-	-	-	-
Williamson	0.00	-0.10	-0.28	-0.43	-	-	-	-	-	-	-

Appendix E. Listing and basic data for the lakes and lake trout populations used to study late-summer lake trout habitat. The latitude and longitude are provided, along with the OMNR administrative district number in which the lake is found. A classification of the population status (see Table 1) and the average percent of the lake trout that are native are indicated. The number of temperature-oxygen profiles used in the study and the area, volume, and maximum depth of the lake are provided.

No.	Lake name	Latitude	Longitude	District	Population status	% native	No. of profiles	Area (ha)	Volume ($\times 10^3 \text{ m}^3$)	Maximum depth (m)
1	Agnes	4813	9120	21	1	100	7	3382.1	39996.1	71.0
2	Allen	4707	7815	32	1	100	1	97.8	838.4	28.0
3	Amos	4708	7834	34	8	0	1	71.7	423.7	28.0
4	Azusaerher	4445	7812	33	3	97	3	633.8	8832.6	41.2
5	Ast	4705	7827	34	3	87	1	126.3	983.3	28.0
6	Ayles	4537	7731	31	1	100	11	2034.6	34937.6	72.9
7	Beley	4707	7721	66	10	0	2	195.1	1366.6	39.0
8	Beptate	4707	7809	32	1	100	2	2226.3	10666.1	52.0
9	Berk	4527	7731	36	6	25	7	3748.5	92369.8	87.3
10	Bernard	4707	7728	66	1	100	2	39.1	739.1	46.2
11	Bay	4701	7732	32	3	78	3	87.4	953.0	25.0
12	Beach	4705	7842	34	3	100	1	134.0	238.4	30.0
13	Beg Chert	4433	7838	64	3	65	3	169.0	3434.2	61.0
14	Beg Hawk	4710	7844	37	3	66	2	365.2	6588.2	56.0
15	Beg Mink	4713	7805	32	3	50	2	196.2	1198.6	23.8
16	Beg Redstone	4711	7832	34	1	100	3	1174.3	24336.0	82.3
17	Beg Redstone	4445	7813	61	3	51	3	6478.2	86137.2	96.1
18	Beg Salmon	4432	7830	64	3	72	3	172.2	2285.3	42.0
19	Beg Trout	4435	7836	34	1	100	2	204.0	1905.6	34.0
20	Bellings	4732	7733	34	3	10	2	240.0	651.7	37.8
21	Berk	4433	7833	64	3	70	2	195.2	3366.0	39.9
22	Bison	4710	7835	34	6	14	2	42.0	512.5	28.0
23	Black (Eyes)	4449	7849	34	6	100	4	67.5	479.4	17.0
24	Black (Lameworth)	4432	7830	34	3	100	1	62.4	603.8	38.6
25	Blue	4433	7732	66	1	100	2	28.6	436.2	30.0
26	Bub	4433	7847	34	3	73	1	23.5	368.3	32.0
27	Buckling	4704	7844	34	3	69	1	716.4	16673.4	68.0
28	Buck	4723	7809	33	3	60	1	36.2	339.4	24.0
29	Burn	4709	7705	36	3	90	3	143.3	1587.3	36.6
30	Camp	4736	7835	33	3	75	1	199.3	2827.5	42.0
31	Canning	4450	7838	34	3	0	3	244.1	1690.6	16.3
32	Cassie	4430	7833	64	3	98	2	291.4	6666.4	45.7
33	Cassino	4703	7847	66	9	0	1	221.0	1302.0	21.3
34	Casson	4730	7745	36	3	100	2	278.2	3372.5	43.0
35	Cochet	4433	7733	32	3	10	3	167.9	1297.6	27.4
36	Conce	4701	7813	32	11	0	2	144.1	376.4	13.0
37	Chandee	4449	7849	32	3	65	2	1888.3	17870.8	80.3
38	Charlton	4430	7840	61	3	10	1	2519.1	43780.7	96.1
39	Charlton	4734	7726	36	3	100	5	115.7	1213.3	23.8
40	Cherry	4445	7813	32	3	25	2	22.4	119.3	16.0

Appendix E. Continued

No.	Lake name	Latitude	Longitude	District	Population status	% native	No. of profiles	Area (ha)	Volume ($\times 10^6 \text{ m}^3$)	Maximum depth (m)
41	Clear	4115	7832	34	1	100	1	167.3	2389.3	42.7
42	Clear	4126	7712	36	3	78	3	1730.5	17329.4	42.7
43	Chico	4019	7852	33	3	70	3	137.6	1596.1	25.0
44	Cia	4441	7915	32	3	60	1	90.3	414.2	18.0
45	Crow	4442	7837	66	3	70	2	441.9	6066.7	36.1
46	Crystal	4443	7829	34	3	36	2	483.2	5422.9	34.0
47	Devin	4447	7843	34	3	13	1	93.8	1086.1	29.9
48	Deer	4102	7836	32	3	40	4	189.7	1610.2	20.0
49	Delano	4132	7834	31	1	100	2	26.1	174.2	16.6
50	Delphi	4106	7822	34	1	100	1	26.4	267.3	28.0
51	Desert	4432	7835	64	3	30	2	402.3	8151.6	68.0
52	Devil	4435	7827	64	3	95	3	1061.5	13356.1	44.3
53	Emerson (Phonetic)	4134	7832	32	3	95	2	165.9	1556.9	20.0
54	Emerson (Phonetic)	4122	7732	32	3	60	2	60.9	1132.2	39.6
55	Dickey	4447	7764	66	3	30	8	2079.0	6709.5	54.0
56	Dickens	4147	7812	31	1	100	11	673.4	5493.2	66.6
57	Dug	4017	6400	47	1	100	1	229.0	3089.0	55.8
58	Dusty	4128	7483	33	8	20	2	152.8	1084.0	29.0
59	Doug	4105	7824	34	3	95	7	1002.7	10007.1	33.0
60	Eagle	4441	7842	66	3	30	2	234.7	1656.7	23.0
61	Eden	4434	7806	32	0	50	1	945.8	6137.3	29.9
62	Edinburgh (L.A.A.)	4100	7715	66	1	100	2	197.1	1970.5	22.9
63	Elliot	4023	8242	41	1	100	2	413.1	10013.9	36.6
64	Elton	4101	7814	34	3	85	2	65.6	335.4	15.0
65	Foley	4120	7911	33	3	70	2	511.5	15632.1	67.0
66	Forney	4139	7710	32	3	70	2	113.6	1020.5	24.4
67	Forney	4105	7812	32	3	40	3	336.1	6036.2	31.0
68	Ford	4100	7812	32	1	100	3	236.0	4400.1	40.0
69	Flick	4635	8247	41	1	100	3	951.0	10633.7	70.1
70	Furman	4836	8154	38	11	0	1	228.7	1577.2	17.4
71	Glamour	4417	7822	34	3	30	2	194.8	1976.0	20.0
72	Gold	4443	7917	34	3	80	1	117.6	4976.7	44.0
73	Gong	4700	8332	64	3	100	3	417.9	5402.1	21.3
74	Gunderson	4454	7823	34	11	0	1	87.4	394.4	18.9
75	Gunderson	4710	8340	60	1	100	3	271.7	2237.1	33.3
76	Gunderson	4704	7814	32	3	40	3	236.4	3325.2	43.0
77	Gunderson (Birmingham)	4715	7815	36	8	60	3	74.0	1262.7	42.0
78	Gunderson	4729	8315	46	1	100	1	300.3	3343.8	39.1
79	Gunderson	4412	7714	66	3	40	2	93.6	734.2	24.1
80	Gunderson	4700	7817	66	9	0	1	162.0	936.1	19.3
81	Gulf	4451	7847	34	3	97	2	905.8	10468.2	70.0
82	Halfway	4123	7736	36	10	0	0	81.6	822.7	26.3
83	Halfway	4112	7824	34	3	86	2	1012.9	17951.6	33.0
84	Hall	4100	7840	34	3	91	2	543.2	13300.6	60.0

Appendix E. Continued

No.	Lake name	Latitude	Longitude	District	Population status	% native	No. of profiles	Area (ha)	Volume (x10 ⁶ m ³)	Maximum depth (m)
85	Havickack	4517	7638	54	8	12	1	176.3	1854.8	30.5
86	Horneshon	4518	7651	55	8	0	1	289.8	2077.9	22.9
87	Hudson	4504	7638	52	3	75	2	73.7	822.0	23.0
88	Hungry	4448	7653	66	5	20	2	234.8	1879.3	32.3
89	Indian	4934	9140	13	1	100	4	1788.0	23133.9	31.1
90	Jamison	4504	7741	52	8	50	2	46.1	387.6	23.8
91	Jeffrey	4501	7753	52	1	100	1	42.1	487.3	36.6
92	Joe Perry	4455	7718	66	3	90	2	168.8	1243.2	22.9
93	Johnson	4516	7637	54	3	28	1	158.0	2886.1	2.7
94	Joseph	4511	7647	53	3	95	3	3133.6	128796.4	93.0
95	Kabakwa	4507	7648	54	8	27	1	113.6	714.8	17.0
96	Kamondog	4525	7741	56	3	69	3	2197.3	20795.9	40.5
97	Kashagwigomog	4459	7636	54	3	30	1	817.9	10895.4	41.0
98	Kashwakamak	4452	7701	66	9	0	1	1172.0	6018.4	21.9
99	Kawagoma	4518	7645	53	1	100	4	2821.0	39918.7	78.0
100	Kelly	4515	7637	54	3	62	1	102.0	1230.2	30.5
101	Kenneth	4513	7638	54	3	82	1	1774.6	31665.6	75.2
102	Kinball	4521	7641	53	3	95	1	212.3	489.2	69.0
103	King	4506	7722	66	10	0	1	36.6	313.6	24.7
104	Kowhion	4427	7637	64	3	70	1	181.7	2799.1	34.7
105	Kushkong	4458	7629	54	8	0	8	496.1	4148.1	42.0
106	Kulan	4528	7744	56			1	1774.6	31665.6	75.2
107	Kushog	4504	7647	57	3	45	1	498.3	6355.3	36.1
108	L'Antrie	4501	7749	52	3	43	1	178.4	4116.0	35.0
109	Lavelle	4457	7756	52	3	25	2	85.0	1082.0	31.1
110	Lavelle	4551	7814	51	1	100	8	2427.6	35863.8	50.0
111	Limerick	4453	7737	52	3	75	3	744.9	6321.0	29.0
112	Limerick	4504	7734	52	3	60	2	52.9	481.6	36.6
113	Lipsy	4519	7638	54	8	5	2	69.0	1214.0	32.0
114	Little Black	4515	7631	54	1	100	3	21.9	166.3	13.3
115	Little Gull	4905	9136	21	1	100	4	325.4	3752.3	36.3
116	Little Hawk	4509	7643	57	3	56	2	344.3	10866.1	95.0
117	Little Kamsau	4515	7635	54	3	46	1	229.6	3120.5	43.9
118	Little May	4503	7736	52	3	25	1	25.3	189.2	17.4
119	Little Mervil	4455	7714	66	9	20	1	36.7	337.3	16.3
120	Long	4441	7610	52	3	75	4	95.3	901.7	26.0
121	Long Mallory	4580	7710	66	9	0	2	63.3	496.3	17.4
122	Long Schwaner	4586	7659	66	9	0	2	280.3	1416.0	20.1
123	Loon	4525	7659	53	3	45	2	31.3	178.0	14.0
124	Loonks	4441	7614	52	3	75	2	34.5	261.8	20.0
125	Loughborough	4423	7632	64	6	0	2	736.2	10834.3	38.4
126	Lovisa	4528	7629	51	1	100	1	489.3	8347.9	41.0
127	Lower Beverly	4436	7638	61	10	0	1	767.0	6668.7	24.4
128	Loyal	4435	7658	66	3	0	1	16.3	227.4	31.0

Appendix E. Continued

No.	Lake name	Latitude	Longitude	District	Population status	% native	No. of profiles	Area (ha)	Volume (x10 ⁶ m ³)	Maximum depth (m)
129	Macdonald	4514	7634	5	1	100	1	145.6	1612.4	39.6
130	Mackie	4505	7659	40	5	40	1	157.8	1793.8	22.9
131	Mamersipewa	4554	9149	13	1	100	1	5330.0	40780.0	48.8
132	Maple	4506	7640	54	5	25	1	324.9	3625.3	39.6
133	Marble	4450	7706	46	10	0	1	175.6	688.2	25.5
134	Marsden	4514	7631	54	10	0	1	230.2	876.5	24.0
135	Mary	4515	7615	53	5	80	1	1066.5	26337.0	55.0
136	Mayo	4502	7735	52	5	40	3	183.1	1638.9	36.1
137	McClelland	4452	7709	46	5	5	2	55.6	449.4	31.1
138	Megunt	4715	8552	44	1	100	5	620.5	4050.1	18.0
139	Mephono	4456	7735	52	5	42	5	151.0	2396.1	42.1
140	Mimamaki	4558	9280	16	1	100	1	157.8	1345.8	22.9
141	Miskawis	4505	7619	54	7	77	1	265.8	3236.1	44.0
142	Missinagaga	4452	7705	46	10	0	1	507.5	4572.1	23.8
143	Missinagwa	4442	7619	54	5	85	1	654.2	11797.0	44.2
144	Momonoch	4454	7612	54	8	0	2	76.6	645.2	16.0
145	Morse	4509	7628	54	5	85	2	289.7	4832.7	42.0
146	Mosque (Switz)	4511	7635	46	8	80	2	157.6	1023.8	15.5
147	Mountain	4459	7645	54	5	25	2	25.0	215.0	18.0
148	Mushoka	4500	7625	53	5	25	2	12215.5	279492.9	86.5
149	Nabe	4643	9130	21	1	100	3	385.4	2754.1	30.0
150	North	4515	7624	54	8	0	2	85.1	1295.6	36.0
151	North Pigon	4455	7647	54	5	45	1	50.1	744.6	39.0
152	Nuckani	4512	7644	57	5	75	4	115.7	930.7	27.0
153	Ohlong	4511	7626	54	5	64	1	97.2	965.5	27.4
154	Opango	4542	7625	51	1	100	11	5154.2	75713.0	49.4
155	Ouar (Cotter)	4504	7725	46	5	20	2	505.6	2655.5	29.5
156	Paguchi	4534	9152	15	1	100	1	1077.0	16670.5	38.0
157	Palmerton	4505	7652	46	5	20	2	562.8	15622.9	56.4
158	Peaback	4458	7605	52	5	50	4	754.8	5503.2	46.0
159	Pough	4535	7742	36	5	100	1	1077.0	16670.5	38.0
160	Pennicote	4520	7686	55	5	20	2	864.8	4515.4	15.0
161	Perrin	4657	9216	12	1	100	1	1197.1	12176.5	16.5
162	Picard	4447	7625	54	5	40	2	75.8	764.1	38.0
163	Pickart	4657	9129	21	1	100	2	1320.0	14201.8	38.4
164	Pindy	4521	7744	52	8	25	2	152.8	1596.8	23.0
165	Pony	4505	7615	52	8	40	3	56.7	58.2	36.0
166	Regan	4526	7731	52	10	0	2	156.8	1596.0	35.1
167	Randy	4454	7720	46	9	0	5	45.2	427.8	17.0
168	Raven	4512	7651	57	5	47	2	589.7	4641.0	44.0
169	Ridbeck	4526	7602	55	5	50	1	250.5	1961.6	28.0
170	Red Horse (East)	4452	7605	45	5	50	1	140.5	1556.0	36.9
171	Red Pine	4512	7642	57	5	95	1	583.9	4108.0	41.0
172	Ridrock	4745	8448	47	8	5	10	287.6	1986.7	20.4

Appendix E. Continued

No.	Lake name	Latitude	Longitude	District	Population nearest	% native	No. of profiles	Area (ha)	Volume (x10 ⁶ m ³)	Maximum depth (m)
173	Rend	4704	7656	36	0	11	4	208.2	411.0	18.6
174	Ridgeway	4670	7725	37	0	0	0	615.1	1090.5	25.1
175	Riverton	4710	7730	37	0	0	0	615.1	1090.5	25.1
176	Riverton	4710	7730	37	0	0	0	615.1	1090.5	25.1
177	Riverton Schwaner	4707	7730	37	0	0	0	2075.1	40022.0	54.0
178	Riverton	4672	7730	37	0	0	0	280.2	2493.3	32.3
179	Riverton	4640	7730	37	0	0	0	20.7	249.3	32.3
180	Shabonika	4650	7730	37	0	0	0	171.0	2047.3	32.3
181	Shabonika	4672	7730	37	0	0	0	207.0	2493.3	32.3
182	Shabonika	4711	7730	37	0	0	0	32.9	302.4	34.0
183	Shabonika	4670	7730	37	0	0	0	272.0	2442.6	32.3
184	Shabonika	4714	7730	37	0	0	0	100.3	772.0	29.0
185	Shabonika	4706	7730	37	0	0	0	240.1	2134.1	24.4
186	Shabonika	4670	7730	37	0	0	0	27.0	207.2	18.6
187	Shabonika	4717	7730	37	0	0	0	1276.1	9824.1	24.3
188	Shabonika	4710	7730	37	0	0	0	21.7	798.9	36.0
189	Shabonika	4710	7730	37	0	0	0	671.3	9801.3	24.9
190	Shabonika	4709	7730	37	0	0	0	96.7	2030.0	36.0
191	Shabonika	4710	7730	37	0	0	0	46.9	313.7	23.2
192	St. Mary	4706	7650	37	0	0	0	364.4	444.4	36.6
193	St. Mary	4704	7650	37	0	0	0	106.3	772.9	24.0
194	St. Mary	4717	7650	37	0	0	0	234.7	2014.8	26.7
195	St. Mary	4670	7614	37	0	0	0	43.7	1113.3	23.3
196	St. Mary	4670	7614	37	0	0	0	46.3	367.0	16.0
197	St. Mary	4646	7614	37	0	0	0	76.1	676.0	24.4
198	St. Mary	4647	7730	37	0	0	0	170.0	1315.6	18.3
199	St. Mary	4674	7636	37	0	0	0	111.7	990.4	24.7
200	St. Mary	4647	7730	37	0	0	0	170.0	1315.6	18.3
201	St. Mary	4741	7646	37	0	0	0	1123.0	12471.1	23.3
202	St. Mary	4640	7614	37	0	0	0	147.9	1196.6	20.4
203	St. Mary	4706	7730	37	0	0	0	27.2	171.1	14.0
204	St. Mary	4700	7744	37	0	0	0	177.0	2112.3	33.3
205	St. Mary	4711	7643	37	0	0	0	177.2	2127.3	43.0
206	St. Mary	4641	7630	37	0	0	0	196.8	4766.9	27.0
207	St. Mary	4714	7630	37	0	0	0	1363.0	11766.3	18.3
208	St. Mary	4736	7710	37	0	0	0	44.0	328.8	26.3
209	St. Mary	4702	7725	37	0	0	0	196.1	1449.3	26.3
210	St. Mary	4710	7646	37	0	0	0	1473.0	17082.0	24.9
211	St. Mary	4705	7730	37	0	0	0	774.8	4074.7	47.3
212	St. Mary	4671	7730	37	0	0	0	21.9	713.8	26.6
213	St. Mary	4713	7633	37	0	0	0	363.3	3463.8	21.3
214	St. Mary	4713	7633	37	0	0	0	106.4	1311.7	24.0

Appendix F. Variables used to partition and compare the relations between the status of various lake trout populations, as well as the percent unmarked, or native, lake trout and the various lake morphological and environmental conditions in the late-summer juvenile and adult lake trout habitat. The habitat and environmental conditions include partitioning various absolute and relative volumes in relation to temperature and oxygen concentration, including preferred, vital, and habitable lake trout habitats, depth distributions, absolute and relative temperature and oxygen concentrations.

Number	Acronym	Definition
0	NAME	Lake name
1	DIST	Ontario Ministry of Natural Resources administrative district number
2	POPSTATUS	Status of the lake trout population based on origin, stocking, reproduction, and recruitment, numerically coded based on categories from "The Lake Trout Atlas"
3	PERUNMARK	Percent of the lake trout sampled from the population that are unclipped, hence are considered to be native
4	NO.PROFIL	Number of temperature/oxygen profiles that are used, entered by date--year, month, day
5	AREA	Total surface area (ha) of lake
6	VOLUME	Total volume ($\times 10^4 \text{m}^3$) of lake
7	MAXDEP	Maximum depth (m) of lake
8	VOLPRE	Volume ($\times 10^4 \text{m}^3$) of preferred lake trout habitat; volume of lake that is 10°C or less and has an oxygen concentration of 6 mg L^{-1} or more
9	PERPRETOT	Volume of preferred habitat as a percent of total lake volume (relative volume--%)
10	MTEMPPRE	Mean temperature ($^\circ\text{C}$) of volume of the lake that contains preferred habitat
11	MOXYPRE	Mean oxygen concentration (mg L^{-1}) of volume of the lake that contains preferred habitat
12	MSATPRE	Mean percent oxygen saturation of volume of the lake that contains preferred habitat (% saturation)
13	DEPRANPRE	Depth range (m) of preferred habitat
14	DEPMEDPRE	Median depth (m) of preferred habitat
15	VOLVIT	Volume of vital lake trout habitat: volume of the lake that is 15.5°C or less and has an oxygen concentration of 4 mg L^{-1} or more ($\times 10^4 \text{m}^3$)

Appendix F. Continued

Number	Acronym	Definition
16	PERVITTOT	Volume of vital habitat as a percent of total lake volume (relative volume--%)
17	MTEMPVIT	Mean temperature (°C) of volume of the lake that contains vital habitat
18	MOXYVIT	Mean oxygen concentration (mg L ⁻¹) of volume of the lake that contains vital habitat
19	MSATVIT	Mean percent oxygen saturation of volume of the lake that contains vital habitat (% saturation)
20	DEPRANVIT	Depth range (m) of vital habitat
21	DEPMEDVIT	Median depth (m) of vital habitat
22	VOLSELT	Volume (x10 ⁴ m ³) of the lake that contains temperatures which, according to the published literature, adult lake trout select in mid-summer, ranging from 8.4 to 10.6°C
23	PERSELTTO	Volume of the lake that contains selected temperature range for adults as a percent of total lake volume (relative volume--%)
24	MTEMPSELT	Mean temperature (°C) of volume of the lake that contains the selected temperature range
25	MOXYSELT	Mean oxygen concentration (mg L ⁻¹) of volume of the lake that contains the selected temperature range
26	MSATSELT	Mean percent oxygen saturation of volume of the lake that contains the selected temperature range (% saturation)
27	DEPRSELT	Depth range (m) of volume of the lake that contains the selected temperature range
28	DEPMSELT	Median depth (m) of volume of the lake that contains the selected temperature range
29	TMPA23M	Temperature (°C) at published mean mid-summer depth (23 m) of adult lake trout
30	OXYA23M	Oxygen concentration (mg L ⁻¹) at published mean mid-summer depth (23 m) of adult lake trout
31	SATA23M	Percent oxygen saturation at published mean mid-summer depth (23 m) of adult lake trout (% saturation)

Appendix F. Continued

Number	Acronym	Definition
32	MDEPA1828	Mean depth (m) of the volume of the lake that represents the 95% confidence limits for the published mid-summer depth distribution of adult lake trout (18-28 m)
33	VOLA1828M	Volume ($\times 10^4 \text{ m}^3$) of lake that contains the mid-summer depth distribution of adult lake trout (18-28 m)
34	PERA1828M	Volume of lake that contains the mid-summer depth distribution of adult lake trout (18-28 m) as a percent of total lake volume (relative volume--%)
35	MTEMPA182	Mean temperature ($^{\circ}\text{C}$) of volume of the lake that contains the mid-summer depth distribution of adult lake trout (18-28 m)
36	MOXYA1828	Mean oxygen concentration (mg L^{-1}) of volume of the lake that contains the mid-summer depth distribution of adult lake trout (18-28 m)
37	MSATA1828	Mean percent saturation of oxygen concentration of volume of the lake that contains the mid-summer depth distribution of adult lake trout (18-28 m) (% saturation)
38	TMPJ33M	Temperature ($^{\circ}\text{C}$) at the observed (JMC) mean mid-summer depth distribution (33 m) of juvenile lake trout
39	OXYJ33M	Oxygen concentration (mg L^{-1}) at mean mid-summer depth distribution (33 m) of juvenile lake trout
40	SATJ33M	Percent oxygen saturation at mean mid-summer depth distribution (33 m) of juvenile lake trout (% saturation)
41	MDEPJ2750	Mean depth (m) of volume of the lake that represents the 95% confidence limits for the published mid-summer depth distribution of juvenile lake trout (27-50 m)
42	VOLJ2750M	Volume ($\times 10^4 \text{ m}^3$) of lake that contains the mid-summer depth distribution of juvenile lake trout (27-50 m)
43	PERJ2750M	Volume of lake that contains the mid-summer depth distribution of juvenile lake trout (27-50 m) as a percent of total lake volume (relative volume--%)
44	MTEMPJ275	Mean temperature ($^{\circ}\text{C}$) of volume of the lake that contains the mid-summer depth distribution of juvenile lake trout (27-50 m)
45	MOXYJ2750	Mean oxygen concentration (mg L^{-1}) of volume of the lake that contains mid-summer depth distribution of juvenile lake trout (27-50 m)

Appendix F. Continued

Number	Acronym	Definition
46	MSATJ2750	Mean percent saturation of oxygen concentration of volume of the lake that contains the mid-summer depth distribution of juvenile lake trout (27-50 m) (% saturation)
47	MDEP64	Mean depth (m) of lake that contains from 6 down to 4 mg L ⁻¹ oxygen--restricted preferred habitat of juveniles
48	VOLUME64	Volume (x10 ⁴ m ³) of lake that has from 4 to 6 mg L ⁻¹ oxygen--restricted preferred habitat of juveniles
49	PERTOT64	Percent of volume of the lake that has from 4 to 6 mg L ⁻¹ oxygen as a percent of total lake volume (relative volume--%)
50	MTMP64	Mean temperature (°C) of volume of the lake that has from 4 to 6 mg L ⁻¹ oxygen
51	MOXY64	Mean oxygen concentration (mg L ⁻¹) of volume of the lake that has from 4 to 6 mg L ⁻¹ oxygen
52	MSAT64	Mean percent oxygen saturation of volume of the lake that has from 4 to 6 mg L ⁻¹ oxygen (% saturation)
53	DEPMAX64	Maximum depth (m) of volume of the lake that has from 4 to 6 mg L ⁻¹ oxygen
54	DEPMIN64	Minimum depth (m) of volume of the lake that has from 4 to 6 mg L ⁻¹ oxygen
55	MDEP62	Mean depth (m) of the lakes that contains from 6 down to 2 mg L ⁻¹ oxygen--restricted vital habitat of juveniles
56	VOLUME62	Volume (x10 ⁴ m ³) of the lake that has from 2 to 6 mg L ⁻¹ oxygen--restricted vital habitat of juveniles
57	PERTOT62	Percent of volume of the lake that has from 2 to 6 mg L ⁻¹ oxygen as a percent of total lake volume (relative volume--%)
58	MTMP62	Mean temperature (°C) of volume of the lake that has from 2 to 6 mg L ⁻¹ oxygen
59	MOXY62	Mean oxygen concentration (mg L ⁻¹) of volume of the lake that has from 2 to 6 mg L ⁻¹ oxygen
60	MSAT62	Mean percent oxygen saturation of volume of the lake that has from 2 to 6 mg L ⁻¹ oxygen (% saturation)

Appendix F. Continued

Number	Acronym	Definition
61	DEPMAX62	Maximum depth (m) of volume of the lake that has from 2 to 6 mg L ⁻¹ oxygen
62	DEPMIN62	Minimum depth (m) of volume of the lake that has from 2 to 6 mg L ⁻¹ oxygen
63	MDEP42	Mean depth (m) of lake that has from 2 to 6 mg L ⁻¹ oxygen--tolerable habitat of juveniles
64	VOLUME42	Volume (x10 ⁴ m ³) of lake that has from 2 to 4 mg L ⁻¹ oxygen--tolerable habitat for juveniles
65	PERTOT42	Percent of volume of the lake that has from 2 to 4 mg L ⁻¹ oxygen as a percent of total lake volume (relative volume--%)
66	MTMP42	Mean temperature (°C) of volume of the lake that has from 2 to 4 mg L ⁻¹ oxygen
67	MOXY42	Mean oxygen concentration (mg L ⁻¹) of volume of the lake that has from 2 to 4 mg L ⁻¹ oxygen
68	MSAT42	Mean percent oxygen saturation of volume of the lake that has from 2 to 4 mg L ⁻¹ oxygen (% saturation)
69	DEPMAX42	Maximum depth (m) of volume of the lake that has from 2 to 6 mg L ⁻¹ oxygen
70	DEPMIN42	Minimum depth (m) of volume of the lake that has from 2 to 4 mg L ⁻¹ oxygen
71	PERFREVIT	Volume of preferred adult habitat (<10°C and >6 mg L ⁻¹ oxygen) as a percent of vital adult habitat (<15.5°C and >4 mg L ⁻¹ oxygen) (relative volume--%)
72	VOLHAB	Volume (x10 ⁴ m ³) of habitable lake trout habitat; volume that is 15.5°C or less and has an oxygen concentration of 2 mg L ⁻¹ or more
73	PERHABTOT	Volume of habitable habitat (<15.5°C and >2 mg L ⁻¹ oxygen) as a percent of total volume of lake (relative volume--%)
74	PER62HAB	Volume of the lake that has from 2 to 6 mg L ⁻¹ oxygen (vital juvenile habitat) as a percent of volume of habitable habitat (<15.5°C and >2 mg L ⁻¹ oxygen) (relative volume--%)
75	PER62VIT	Volume of lake that has from 2 to 6 mg L ⁻¹ oxygen (vital juvenile habitat) as a percent of volume of vital adult habitat (<15.5°C and >4 mg L ⁻¹ oxygen) (relative volume--%)

Appendix F. Continued.

Number	Acronym	Definition
76	PER42HAB	Volume of lake that has from 2 to 4 mg L ⁻¹ oxygen (tolerable juvenile habitat) as a percent of volume of habitable habitat (<15.5°C and >2 mg L ⁻¹ oxygen) (relative volume--%)
77	PER64HAB	Volume of lake that has from 4 to 6 mg L ⁻¹ oxygen (preferred juvenile habitat) as a percent of volume of habitable habitat (<15.5°C and >2 mg L ⁻¹ oxygen) (relative volume--%)
78	VOLL2	Volume (x10 ⁴ m ³) of lake that contains 2 mg L ⁻¹ or less oxygen
79	VOLL15.5	Volume (x10 ⁴ m ³) of lake that is 15.5°C or less
80	PERL2TOT	Volume of lake that contains 2 mg L ⁻¹ or less oxygen as a percent of total volume of lake (relative volume--%)